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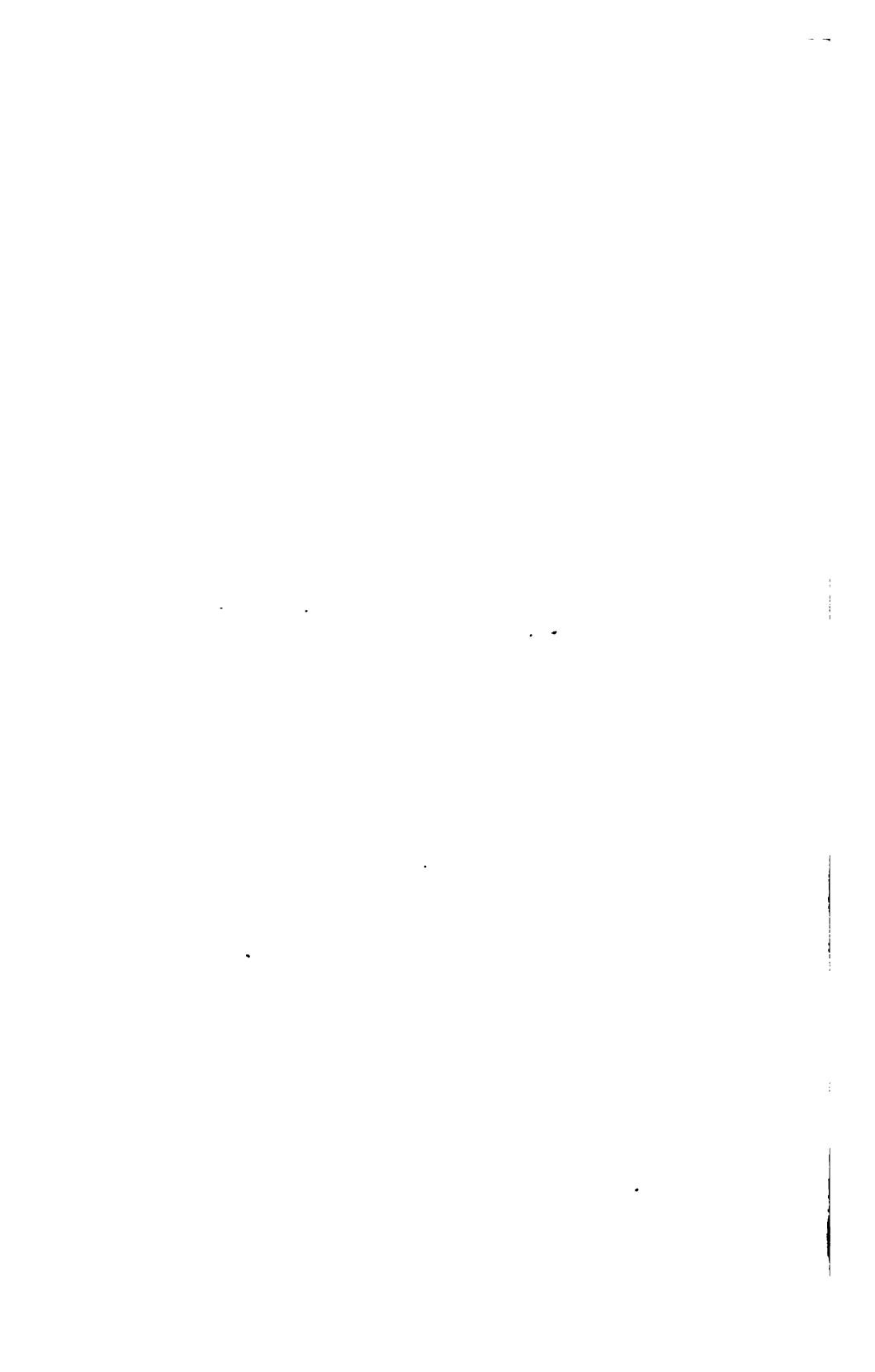
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THE
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Journal of Anatomy and Physiology.

THE ANATOMY OF THE MUSCLES, LIGAMENTS, AND FASCIÆ OF THE ORBIT, INCLUDING AN ACCOUNT OF THE CAPSULE OF TENON, THE CHECK LIGAMENTS OF THE RECTI, AND OF THE SUSPENSORY LIGAMENT OF THE EYE. By C. B. LOCKWOOD. (PLATE I.)

THE surgical and physiological importance which belongs to the anatomy of the orbit is so considerable, that anatomists of acknowledged repute have devoted themselves to its investigation. Hardly any fact of importance has escaped the attention of at least one observer; and any addition to the literature of the subject might seem needless, were it not that the greatest difference of opinion prevails upon many interesting points. The writer is not so presumptuous as to think that his decisions will be accepted where eminent men have disagreed, but it may be deemed of service if the various statements are collated, and, where necessary, amplified and explained.

Posterior Attachments of the Muscles of the Eye.—At the beginning of the present century Tenon wrote that the labours of Zinn, Sabatier, and Portal left nothing to be said concerning the posterior attachments of the muscles of the eye.¹ The first-mentioned author, Zinn,² described “a ligament common to the inferior, internal, and external recti,” but the accounts of this

¹ *Memoire et Observations sur l'Anatomie, la Pathologie et la Chirurgie*, Paris, 1806, p. 195.

² *Descriptio Anatomica Oculi Humani*, Goettingæ, 1780, p. 148. Paragraph, “De ligamento communi unde oriuntur muscoli adducens, deprimens et abducens caput alterum.”

structure given in English text-books,¹ are not free from ambiguity and often lead to misapprehension. The source of error seems to be in the word "ligament," which Zinn applied to his discovery; but he afterwards speaks of it as "*tendinem verum splendentem*," clearly implying its tendinous appearance. M. Sappey² always calls it the tendon of Zinn, and writes of it as follows:—"A fibrous cord which is attached to a very small fossa situated beneath and external to the optic foramen. This cord speedily divides into three slips—a middle, which goes to the inferior rectus; an inner, to the internal rectus; and an external, to the external rectus. Of these three bands the middle is the largest." It may be added that the fasciculus, which belongs to the external rectus, is prolonged up the posterior border of the muscle, and ends by blending with the origin of the superior rectus. The accompanying diagram, made from a dissection, may serve to give an idea of this structure (Plate I. fig. 1). The preparation from which it was taken was made in the following way:—The roof of the orbit was freely removed, so as to include the lesser wing of the sphenoid and the upper part of the optic foramen. The muscles having been exposed and cleaned, the levator palpebræ was divided from its posterior attachments and turned forwards. Next, the superior rectus and superior head of the external rectus were cut from their "apparent" origin, from the sheath of the optic nerve, and turned outwards. By this means the sheath of the optic nerve was exposed, divided in the optic foramen, and, together with its contents, removed. A little loose cellular tissue having been taken away, the part delineated was laid bare. It will be seen that the figure does not quite conform to M. Sappey's description, but, as is not infrequently the case, there is a slight departure from the normal.

A little reflection shows that the origins of the ocular muscles have not been studied from quite the same point of view. For instance, the group which comprises the inferior rectus, the lower part of the internal rectus, and the inferior head of the external rectus, has invariably been described with special reference to

¹ Quain's *Anatomy*, 8th ed., 1882, p. 281; also Gray's *Anatomy*, 10th ed., 1883, p. 212.

² *Traité d'Anatomie Descriptive*, Paris, 1876, p. 101 *seq.*

their inner surface, *i.e.*, that which is next the optic nerve; whilst the upper group, that which comprises the superior rectus, the upper part of the internal rectus, and superior head of the external rectus, has always been described with special reference to their external or orbital aspect.¹

Each anatomist seems to have omitted to inspect the ocular or underneath surface of the upper group of muscles, although they all describe that part of the lower. This omission was repaired in the following manner:—

Orbits were taken intact from skulls which had been frozen as Dr Garson directs,² and horizontal sections were made through about the centre of the cornea and the centre of the optic foramen. The upper part of the orbit and its contents were then dissected in the usual manner. The optic nerve and its sheath together with loose connective tissue having been removed, it became evident that the under surface of the superior rectus possessed a tendon very similar to that of the inferior rectus. The structure is fastened to the upper and outer margin of the optic foramen. Anteriorly it is aponeurotic, and gives attachment to the superior rectus, the upper part of the internal rectus, and the superior head of the external rectus. The fasciculus, which belongs to the latter muscle, passes down its posterior border, and is continuous with the slip which this muscle receives from the tendon of Zinn. It will be seen from the diagram (Plate I. fig. 2), which I have made from a preparation, that the structure in question bears a strong resemblance to the tendon of Zinn; but, so far as I can ascertain, no observer has mentioned it.³

¹ The writings of Zinn (p. 148), Portal (*Cours d'Anatomie Médicale*, Paris, 1808, tome ii., p. 62), and Sabatier (*Traité Complet d'Anatomie*, Paris, 1791, tome ii., p. 82) shows this to be the case so far as they are concerned. The modern authors Henle (*Handbuch der Eingeweidelehre des Menschen*, Braunschweig, 1878, p. 713), Hyrtl (*Handbuch der Topographischen Anatomie*, Wein, 1882, Erster band, p. 223), Cruveilhier (*Traité d'Anatomie Descriptive*, Paris, 1874, tome ii., p. 622 *seq.*), Sappey (p. 97 *seq.*), Quain (p. 281), and Gray (p. 212), have with little exception followed in the footsteps of their predecessors.

² *Human Morphology*, Reeves, London, 1st ed., i. 79.

³ Merkel (Graefe und Saemisch, *Handbuch der Gesammten Augenheilkunde*, Erster band, Leipzig, 1874, p. 52), who undertook, he says, an original investigation of these origins, mentions tendinous fibres other than the ligament of Zinn, but it does not seem, from his account, that they are at all identical with the common tendon which has just been described and figured.

The conclusion arrived at, after studying the origins of the recti from every aspect, is that their orbital surfaces look fibrous, and seem intimately blended with the sheath of the optic nerve and the fibrous tissue which surrounds the optic foramen; examined from their inner ocular aspect, they look tendinous, and may be said to arise by a superior and inferior common tendon.

The Capsule of Tenon.—Since the way in which the capsule of Tenon is dissected has an important bearing upon the result, those which have usually been adopted will be mentioned. Tenon says—

“Saw off the skull-cap, following a line which passes immediately above the roof of the orbit; take away the posterior part of the skull as far forward as the optic foramen; separate the right from the left half of the face by a saw-cut passing through the nose; next, with a very fine saw, such as clockmakers use, saw the roof of the orbit from the internal angle to the optic foramen, and from the external angle to the same aperture; when this has been done, raise the portion of the bone, which is triangular, with its apex at the optic foramen, turn this fragment of bone over the upper eyelid without detaching the latter, then detach each of the muscles from around the optic foramen and optic nerve, raise their posterior extremities and dissect them with care from behind forwards; soon you will recognise the capsule in question.”

Ferrall¹ says—“Divide the palpebræ vertically, and, turning the separate portions backwards towards the forehead and cheek respectively, fix them in their position by hooks; the conjunctiva is next divided at its angle of reflection, where it passes from the internal surface of the eyelid to the ball of the eye. . . .” After commenting upon the inaccuracies of the previous descriptions of Zinn, Sœmmering, and Lawrence, he proceeds—“Having, however, separated the divided conjunctiva, we expose, not as has been described by anatomists, a cushion of adipose tissue but a distinct tunic of a yellowish-white colour and fibrous consistence, continuous in front with the posterior margin of the tarsal cartilage, and extending backwards to the bottom or apex of the orbit (?) where its consistence becomes less strongly marked. By proceeding in the manner I have mentioned, the parts are displayed without any elaborate dissection. The sharp end of the probe or director will be sufficient to separate the ball of the eye from the new organ, by probing gently the fine cellular tissue which connects them.” Bonnet² adopts almost exactly the same method; but it will afterwards be seen that he did not obtain quite the same results. It may be stated at once that the dissections of Tenon, Ferrall, and Bonnet have been carried out by the writer, and

¹ *Dublin Journal of Med. Science*, 1841, p. 336.

² *Séctions Tendineuses et Musculaires*, Paris et Lyons, 1841, p. 8.

serve to confirm, in a great measure, what they have stated. In addition, frozen sections of the orbit have been freely used. It seems quite unnecessary to dwell upon the advantages of this method. It greatly facilitates a very difficult dissection, and enables everything to be seen in its proper relation. The preparations were made in the manner described by Dr Garson. Entire heads were frozen and the orbits removed from them intact by appropriate saw-cuts. Vertical and horizontal sections were afterwards made, the parts being of course still firmly frozen. Any additional steps required to display the various structures will be indicated when they are treated in detail.

The Capsule of Tenon and Insertions of the Ocular Muscles.—The insertions of the ocular muscles are so intimately related to the aponeurosis which surrounds the sclerotic that it will be best to consider these insertions and the aponeurosis together. In studying the capsule of Tenon it is convenient to examine its exterior first. When the orbit is dissected in the customary manner, the membrane may be distinguished by its yellowish colour and closely matted appearance. When the levator palpebræ has been divided, the structure in question is quite easily separated from the orbital fat. When this has been done, three parts will be found to demand attention :—(1) A central part which surrounds the globe ; (2) the prolongations which this sends along the muscles of the eye ; and (3) its connections with the walls of the orbit¹ (Plate I. fig. 3).

Exterior of the Central Portion of the Capsule of Tenon.—Assuming that the orbit has not been treated with alcohol or any hardening solution, the central part of the capsule of Tenon may easily be seized and dragged from the sclerotic. From this it might be inferred that it is merely a loose and thin covering ; but as only the upper and back portion can be approached in this way such a conclusion is hardly warranted. When vertical and horizontal sections are viewed, much more comprehensive ideas may be formed (Plate I. figs. 3 and 4). It is then perceived to be a fibrous capsule² which surrounds the globe from the ciliary margin of the cornea backwards to the entrance of the optic nerve ; its anterior third is intimately related to the back of the ocular conjunctiva ; its middle third sends prolongations to the muscles of the eye ; its posterior third is in contact with and

¹ *Vide Sappey*, p. 105.

² Its strength and appearance were accurately indicated by Ferrall when he called it the “*tunica vaginalis oculi*.”

loosely adherent to the orbital fat.¹ In addition, it is attached, in a manner which will be indicated, to the inner and outer sides of the orbit. Its thickness is not the same in every part, for it is strengthened by various fibrous bands, which require special description, but it is easy to see that it becomes thinner posteriorly, and is continuous with the sheath of the optic nerve, both structures being fastened to the sclerotic. The capsule is adherent for about the space of a quarter of an inch around the margin of the lamina cribrosa. The anterior attachments of the capsule of Tenon are more complicated, and cannot be dismissed so briefly. They have been variously described,² because a clear distinction has not been drawn between the ocular portion of the capsule and the underneath part of the sheath of the levator palpebræ muscle (Plate I. fig. 4).

The anterior third of the ocular portion of the capsule of Tenon blends intimately with the ocular conjunctiva, and together with it is fastened to the ciliary region of the sclerotic (Plate I. figs. 3 and 4). The thin membrane which the union of the conjunctiva and capsule forms may easily be separated to within an eighth of an inch of the margin of the cornea, but any further endeavour entails laceration. In order to avoid misconception, perhaps a further account of the anterior attachment may be permitted. In vertical sections of the orbit the ocular part of the capsule of Tenon seems to blend with the upper and lower fornix of the conjunctiva. Very slight manipulation is required to make it divide at this point—half going, with the conjunctiva, to the sclerotic; half, with that membrane, to the tarsal cartilages. That this manner of dissection, however, is somewhat artificial, is shown by examining horizontal sections. There is no fornix conjunctivæ in these, and the capsule simply blends with the mucous membrane to pass to its insertion on the globe (Plate I. fig. 3). Together with the capsule of Tenon the ocular conjunctiva constitutes a thin layer, separable, except near the margin of the cornea, with the greatest ease from the sclerotic and tendons of the subjacent muscles; but it is practically impossible to divide the ocular conjunctiva near the cornea without opening the interior of the capsule.

¹ Sappey, p. 106.

² Bonnet, p. 16; also Lenoir, "*Des Operations qui se pratiquent sur les muscles de l'œil*," Paris, 1850, p. 10.

The capsule of Tenon was discovered about 1803, and frequent reference will be made to the singularly clear account contained in Tenon's *Memoire* (p. 193). It was forgotten for many years, and Hyrtl (p. 227) says that Malgaigne has the credit of having again brought it into notice. (For Malgaigne's account see his *Traité d'Anatomie Chirurgicale*, i. p. 692.) This author named it the orbital aponeurosis. Next, Bonnet wrote an elaborate description of it, and pointed out its great surgical importance (*Sections Tendineuses et Musculaire*, Paris et Lyons, 1841, p. 8). The labours of this observer have been held in such esteem that the aponeurosis is not infrequently called, after his name, "The capsule of Bonnet."¹ In the remainder of this paper the expression "capsule of Tenon" will be applied to the whole of the capsule. As far as can be ascertained, English anatomists do not appear to have paid minute attention to this subject. In 1841 a very excellent account was published by J. M. Ferrall in the *Dublin Journal of Medical Science*, 1841, p. 336. This surgeon was evidently unaware of Tenon's discoveries. The name "tunica vaginalis oculi" which he gave it seems very appropriate. Mackenzie (*The Cure of Strabismus by Surgical Operation*, London, 1841, p. 11) briefly described the capsule, quoting the accounts of previous writers. With the exception of Ferrall and Bonnet, none of the authorities who have been mentioned made any notable addition to Tenon's original discoveries.

The Muscular Prolongations of the Capsule of Tenon and Check Ligaments of the Internal and External Recti.—Six muscles receive prolongations or sheaths from the capsule of Tenon—the four recti, the superior and inferior oblique. These prolongations spring from the middle third of the capsule, and pass backwards along the recti as far as their middle, where they blend insensibly with their perimysium. The sheath for the superior oblique surrounds its reflected tendon as far as the pulley, and is there attached. The prolongation to the inferior oblique descends upon the muscle as far as the floor of orbit, where it ends. When the inferior oblique is dissected from the front its sheath is about a quarter of an inch long, and at its origin from the capsule of Tenon is yellowish and opaque, but gradually becoming thinner; at last it ends in an exceedingly delicate transparent membrane, which surrounds the rest of the muscle as far as its origin from the superior maxilla. This delicate

¹ Soelberg Wells (*Diseases of the Eye*, London, 1859, p. 587), speaking of this structure, says—"The posterior portion of the sheath, up to the passage of the tendons, has been called the capsule of Bonnet, the anterior portion, from the passage of the tendons to its insertion into the sclerotic, having been designated the capsule of Tenon."

transparent sheath is occasionally attached to the wall of the lachrymal sac.¹

So far the anatomy of the muscular sheaths is easily ascertained and does not admit of much controversy. But, concerning the connections between the sheaths and the muscles they embrace, and between the sheaths and neighbouring parts, great divergence of opinion prevails. I will, therefore, consider their connections *seriatim*, beginning with the external and internal recti.

If the orbit is dissected in the usual way, or if one of the horizontal frozen sections be examined, it is easy to ascertain that, where the internal and external recti pass between the eye and the orbit, they are, in some way or another, attached to both.

The tendons of the muscles lie within the capsule of Tenon, and may be left for future consideration. The structures which connect the inner and outer recti to the malar and lachrymal bones are usually called the "internal and external check ligaments." The reason for this designation will be found in what follows. Of these check ligaments that which belongs to the external rectus is the strongest and easiest to dissect, and will be dealt with first.

It is a wedge-shaped structure about half an inch in length, and as wide as the muscle to which it belongs. The base of the wedge is fastened by a vertical attachment to the malar bone and suspensory ligament of the eye (p. 18); the apex is continuous with the sheath which the external rectus receives from the capsule of Tenon and with the muscle itself, the point of union being situated just behind the place where the muscle becomes tendinous.

Numerous muscular and tendinous fibres pass from the rectus externus into its check ligament, so that the part of the ligament in proximity to the muscle has a distinctly muscular and tendinous appearance, but near its bony insertion this is lost, and it looks yellow and matted. In dissecting-room specimens the muscular prolongations to the ligaments are sometimes hard to

¹ Merkel (p. 58) denies that the sheath of the inferior oblique reaches the floor of the orbit. Sappey (p. 108) mentions the attachment to the bone, and also that to the lachrymal sac.

see, but I have never failed to find them in frozen sections. The check ligaments of the internal rectus differs in no important particular from that which has just been described; it is somewhat smaller and thinner, and is attached to the lachrymal ridge¹ and suspensory ligament of the eye.

In conjunction with Dr V. D. Harris I have examined the microscopic structure of these ligaments. When portions of them were treated with acetic acid nothing but fine elastic fibres could be seen. Fearing lest this might not be deemed sufficient, they were hardened in alcohol and stained in logwood. It was again clear that fine elastic tissue constituted by far their greatest part, not however the whole, for it is to be remembered that they have been stated to contain prolongations of the muscles. Although the preponderance of elastic fibres in them was exceedingly great, nuclei were seen which strongly resembled those of unstriped muscle, but these were too few to permit any confident assertion being made concerning them. The observation that these ligaments are made of elastic fibres lends great significance to Lenoir's remark that "the insertions are by accessory tendons, perhaps even elastic," and to an observation of Tenon's already quoted, in which he says, "they are singularly supple and elastic."

Functions of the Ligaments which connect the Internal and External Recti to the Walls of the Orbit anteriorly.—At least two functions have been attributed to the elastic check ligaments. They have been said by Tenon (p. 197) to alter the direction of the muscles, and prevent them, when in action, from pressing on the globe. They have also been stated to act as check ligaments to limit the retraction of the recti, and prevent them rotating the eye too much.² I think that a rigorous examination of the anatomical conditions upon which the first theory rests will lead to its rejection. Doubt has been cast upon it by Cruveilhier (p. 628), but he adduces no reasons for his opinion, so that, although the pressure theory has met with general acceptance, I would urge the following arguments against it:—The internal and external recti diverge from their origin until they reach the equator of the eye, and then, applying themselves to the sclerotic, converge to gain their insertions.

¹ Sappey, p. 108; also Henle, p. 719, fig. 556.

² Merkel, p. 59.

Each muscle, when it contracts, rotates the globe upon an axis drawn perpendicularly through its centre, but before it can produce this movement it must overcome, at least, the tonic resistance of its antagonist, *i.e.*, the other rectus. Obviously the force which is required to do this must be transmitted through the globe. In other words, each rectus presses upon the equator of the eye with a pressure equal to the tonic resistance of its antagonist. If this is true, it is clear that the mechanical arrangement which actually exists is such that, in the absence of any pressure-preventing apparatus, the eye must to a certain extent be squeezed whenever the recti contract. It need not be repeated that in the elastic ligaments a pressure-preventing apparatus has been recognised. The examination of horizontal frozen sections will show whether they conform to the required conditions. Taking origin from the wall of the orbit almost exactly opposite the equator of the globe, they run backwards nearly half an inch, and then become continuous with the muscles; this union is far behind the place where the latter begin to be in contact with the eye—indeed it is where they are still diverging to reach it; so that it renders the ligaments quite inefficacious for preventing pressure upon any part of the globe (Plate I. fig. 3).

If it is right to assume that the pressure of the muscles would be injurious to the eye, and that, in default of any restraining mechanism, the equator would bear the brunt, we may infer the place at which the required apparatus should be found. When the interior of the capsule of Tenon is described, it will be seen that such ligaments exist.

The statement that the elastic ligaments are of service to check the action of the recti is founded upon much better evidence than the theory which has just been discussed. If the muscles and ligaments be exposed in a fresh orbit, traction exerted upon the muscles makes the ligaments tense. Merkel (p. 59) points out that when they have been divided an excessive rotation of the eye is permitted. It therefore seems appropriate to call them the "internal and external check ligaments," understanding that they check the contraction of the muscles but do not prevent them pressing upon the globe.

It is convenient, before proceeding further, to mention that all

the muscles of the eye are united by connective tissue and by muscular and tendinous fibres to the sheaths which they receive from the capsule of Tenon. The former attachment always exists, but the latter, although it is never absent when frozen sections are examined, may appear very scanty. As regards the object of these insertions of the muscles into the capsule of Tenon, they have been ingeniously compared to such muscles as the sub-crureus, sub-anconeus, &c.¹

Great difference of opinion prevails as to the nature of the anterior attachments of the recti to the walls of the orbit. Tenon remarks that they were known to Zinn, and says they are in part prolongations of the muscles themselves; he calls them "faisceaux tendineux" because of their mixed appearance. Bonnet (p. 23) and Lenoir (p. 10) agree with Tenon, but Malgaigne (p. 703) denies their tendinous characters, and speaks of them as "pretendues tendons"; he also remarks that most French writers, including Tenon, failed to understand them. Sappey (p. 103), speaking more particularly of that which is external, says—"It is continuous at its point of origin with the fibrous sheath of the muscle, and never with the latter, as Tenon thought, and after him a great many authors." This writer proceeds to say they are neither tendons nor ligaments, but unstripped muscles, and names them the external and internal orbital muscles. That the check ligaments receive prolongations from the muscles into which they are inserted has been noted by many authors. Cruveilhier (p. 626) mentions the fact, but does not consider the presence of prolongation so constant as I have stated to be the case. Such an opinion might be formed if the muscles were dissected in the usual way, but frozen sections show that muscular prolongations are the rule. Lenoir (p. 13) also says that "the sheaths of the muscles adhere to them by a dense tissue in which are sometimes found tendinous and muscular bands." Henle makes similar statements, and depicts the tendinous prolongations (fig. 556, p. 719, and fig. 557, p. 721). As far as their structure is concerned, nearly all authorities, except Sappey, agree in calling them ligaments, implying, it may be supposed, that fibrous tissue enters largely into their composition. If it could be substantiated that the check ligaments contained unstripped muscle, and a sufficient quantity of it to pull forwards the recti, and with them the capsule of Tenon, important pathological problems would be solved.

Relations of the Superior Rectus to the Capsule of Tenon and Levator Palpebræ.—The prolongation which the capsule of Tenon sends backwards along the superior rectus differs in no important particular from those already described, but, of course, check ligaments like those of the inner and outer recti are wanting. Almost all authors are agreed that the superior rectus

¹ Merkel, p. 58.

is connected both to the superior tarsal cartilage and to the levator palpebræ, which is in contact with its upper surface, but they differ as to the manner in which it occurs. For instance, Lenoir (p. 10) says that the superior rectus is actually united by muscular and tendinous fibres to the superior tarsal cartilage and levator palpebræ, whilst Cruveilhier (pp. 624 and 614) and Bonnet (p. 26) affirm that the rectus is fastened to them by means of its sheath. This slight difference of opinion is easily explicable, and seems to be due to the fact that these anatomists have ignored the existence of a sheath which surrounds the front part of the levator palpebræ.¹

In order to show how this omission could cause a difference of opinion, I will endeavour to describe the investment of the levator palpebræ, but it cannot be properly appreciated without a preliminary allusion to the anatomy of the muscle. The levator palpebræ is more or less like an isosceles triangle, the apex of which is behind at its origin, and the other angles in front, where they are attached to the rim of the orbit just behind the internal and external tarsal ligaments, with which they are continuous. The sides of the triangle are concave; the inner winds round in contact with the sheath of the tendon of the superior oblique, the outer touches the capsule of the lachrymal gland; the base of the triangle, which is in front, is attached to the upper tarsal cartilage. Owing to its structure and appearance the anterior third of the muscle is called the palpebral aponeurosis. The sheath of the levator palpebræ invests the belly of the muscle for at least half an inch before it, the levator, becomes aponeurotic, and there is no difficulty in demonstrating all its connections either upon frozen sections or by dissecting the orbit from in front. If the latter method be adopted, the roof of the cavity having been taken away, the upper eyelid should be removed layer by layer. Under the tarsal ligament a little yellow fat is found, and, beneath it, the levator palpebræ enclosed in a fairly thick investment of connective tissue. This sheath blends with the perimysium behind, and in front is strongly adherent to the palpebræ aponeurosis; its inner side is inseparable from the sheath of the reflected tendon of the

¹ Ferrall (p. 334) alludes to this sheath in a cursory manner, but does not describe it.

superior oblique, whilst its outer side is fastened to the capsule of the lachrymal gland, which overlies it. The part of the sheath which covers the under surface of the levator palpebræ is fairly thick, and is best examined in vertical frozen sections; anteriorly, it is firmly attached to the back of the palpebral aponeurosis close to the tarsal cartilage and palpebral conjunctiva; posteriorly, it unites at an acute angle with the sheath which the superior rectus receives from the capsule of Tenon (Plate I. fig. 4). Since both the superior rectus and levator palpebræ are intimately adherent to their respective sheaths, it is clear that, where these are continuous, a bond of union must exist between the two muscles. But, besides being connected to the levator palpebræ in this manner, the superior rectus sends muscular and tendinous fibres into the acute angle, or wedge formed by the union of its sheath with that of the levator; some of these fibres pass along the sheath of the levator palpebræ, and through it are connected to the palpebral aponeurosis and superior tarsal cartilage; others, by running forwards along the sheath of the rectus, reach the ocular portion of the capsule of Tenon. It depends upon the quantity of fibres which the rectus sends to the sheath of the levator palpebræ whether it should be considered to be connected to the tarsal cartilage by muscular fibres or by sheath. Except behind, where it unites with the sheath of the superior rectus, the underneath part of the sheath of the levator palpebræ is in contact with, but not united to, the ocular portion of the capsule of Tenon.

The manner in which the superior rectus is united to the levator palpebræ and upper lid having been discussed, the palpebral aponeurosis affords material for consideration. The anatomy of this structure has been sketched already. Its outer and inner orbital attachments, which have been named the internal and external orbital fasciæ,¹ are fastened to the rim of the orbit on a level with the tarsal ligaments (*tendo oculi internum et externum*), whilst its lower margin ends upon the cartilage of the lid. Just before its termination the aponeurosis is strengthened by a transverse band of fibres stretched from side to side across the front aperture of the orbit; and the extremities of this band constitute the internal and external

¹ Cruveilhier, p. 622.

orbital fasciæ, and when the levator palpebræ is pulled upon, the use of these fibres is evident. Owing to their attachments and direction they limit the retraction of the muscle, or, in other words, act as a check ligament.¹ They aid, moreover, in bringing about another result, for, as Cruveilhier points out,² "the movements of the lid, singularly limited at the sides by the orbital insertions of this muscle (levator palpebræ), is a movement of rotation which it performs round the transverse axis of the eye, like the visor of a helmet."

The importance of the connection between the superior rectus and levator palpebræ is now apparent. Owing to their mutual adhesion, one check ligament (the palpebral aponeurosis) serves for both, and besides, the rectus is enabled to lift the upper eyelid. The transverse band which strengthens the palpebral aponeurosis, when examined microscopically, appears throughout to consist of white fibrous tissue.³

The palpebral aponeurosis has another peculiarity which has hardly been recognised. As far as can be judged from a limited number of dissections, it consists of two layers. These are easily perceived in vertical sections, or when the dissection is made from the front. In the latter case, it is best to open the sheath of the muscle at the inner edge, where the layers may be easily separated. The anterior layer is inserted into the middle of the front surface of the tarsal cartilage, the posterior layer is continuous with the upper edge of the cartilage. A little loose connective tissue is found between the two layers of the levator palpebræ, except at the outer side, where the fore part of the lachrymal gland (glandula lachrymalis inferior) intervenes between them.⁴ It might not be unreasonable to speculate whether this relation has anything to do with the secretion of tears. But although the levator palpebræ seems quite adapted to squeeze the lower part of the lachrymal gland, yet it is unlikely that the muscle could alter the position of the gland itself. There is a ligamentous union between the external surface of the lachrymal gland and

¹ Tenon, p. 199.

² Cruveilhier, p. 622.

³ Great difference of opinion exists upon this point. The matter has had full discussion at the hands of Sappey (p. 98) and Cruveilhier (p. 622). The former asserts that it consists of unstriated muscle, and names it the "orbito-palpebral muscle," whilst the latter is of opinion that it is fibrous.

⁴ This interesting fact has been depicted by Sappey, p. 98, fig. 251.

the outer wall of the orbit, which would effectually prevent any movement. It seems appropriate to call these bands the "ligament of the lachrymal band."

Like all other muscles of the orbit, the levator palpebræ sends muscular and tendinous fasciculi to its sheath, which has been shown already to blend with those of the superior rectus, superior oblique, and with the capsule of the lachrymal gland. This circumstance explains many so-called abnormalities.¹

It is hardly within the scope of this paper to discuss the anatomy of the unstriped muscles, superior and inferior palpebral, which are said to enter into the formation of the eyelids.² They have hardly any bearing upon the questions which have been raised.

Relations of the Inferior Rectus to the Capsule of Tenon, Inferior Oblique, and Lower Eyelid.—In general characters the sheath of the inferior rectus is the same as the others. Vertical frozen sections clearly display its arrangement (Plate I. fig. 4). Its upper part has no peculiarity, but merely unites anteriorly, at an acute angle, with that part of the capsule of Tenon which embraces the posterior hemisphere of the eye. The under part of its sheath may be said to consist of two superimposed layers—a superior and inferior (Plate I. fig. 4). If these are followed backwards, they will be found to unite at a very acute angle, into which the muscle sends numerous fasciculi. If the two layers of the underneath part of the sheath of the rectus be traced forwards, they separate; the superior layer keeps in contact with the under surface of the muscle, and is continuous with that part of the capsule of Tenon which supports the anterior hemisphere

¹ Professor Macalister, in his monograph "On Muscular Anomalies in Human Anatomy" (*Transactions of the Royal Irish Academy*, xxv., 1875, p. 7 seq.) says—"The levator palpebræ superioris I have seen joined to the superior rectus as described by Albinus. . . . A muscle has been more recently described as the tensor trochleæ by Professor Budge (Henle u. Pfeufer's *Zeitschrift*, Reihe 3, Bd. vii. p. 273) which is a lateral offshoot from the levator palpebræ superioris inserted by several slips into the trochlea for the superior oblique tendon. . . . I have seen it attached to the upper margin of the tarsal cartilage. Into the tarsal cartilage and into the conjunctiva of the superior palpebral sinus; into the latter alone; into the ciliary fibres of the orbicularis palpebrarum, or into all three." It might be anticipated that, as the sheath of the levator palpebræ is adherent to that of the lachrymal gland fibres of the muscle might have been described going to the latter, but so far I have found no record of any.

² Cruveilhier, p. 614.

of the eye; the inferior layer is inserted into the posterior border of the sheath of the inferior oblique (*vide* fig. 4). So far this account is almost in accordance with what has been stated by others (Merkel, p. 58). The part which goes to the inferior oblique is sometimes considered a direct continuation of the muscle (Cruveilhier, p. 624), but I have described it in accordance with its anatomical appearance, and without regard to its supposed functions. These will be discussed presently. Further, by means of the lower part of its sheath, the inferior rectus forms connections with a structure, which probably has a very important influence upon its action, and which will now be described as follows:—

The Suspensory Ligament of the Eye.—Before endeavouring to describe the suspensory ligament systematically, its rough anatomy may be sketched, and, in doing so, it is hoped that its claim to be considered a distinct ligament may be substantiated.

It may, therefore, be stated that the suspensory ligament is a band of fibrous tissue, stretched, like a sling, from one side of the orbit to the other. The fibres which compose it converge at each end to be inserted into the malar and the lachrymal bones; in the middle they diverge to form a shallow cup upon which the eye rests. The widest part of the suspensory ligament is intimately woven with the capsule of Tenon, but not to such an extent as to conceal the identity of its fibres. In order to ascertain this, the lower eyelid should be removed layer by layer, until nothing is left but the tarsal cartilage and conjunctiva. After a little fat has been taken away from the neighbourhood of the inferior oblique muscle, many of the fibres of the ligament are easily seen crossing in front of the muscle. A more correct opinion of the relations of this ligament to adjoining parts, and especially to the globe, may be derived from a vertical section made through the long axis of the eye. In this the lower part of the capsule of Tenon will be found notably thickened, and (Plate I. fig. 4) the extent of this thickening may be indicated by saying that the lower quarter of the circumference of the globe rests upon it. The thickened portion of the capsule of Tenon is divided by an aperture through which the inferior rectus passes. The posterior part, and this is a very significant point, is thickest just behind this opening, but it gradually

becomes thinner as it passes round the eye; whilst the anterior part looks crescentic, and sends a long thin horn backwards beneath the inferior rectus, forming the upper layer of the under part of its sheath, and another forwards to become continuous with the ocular conjunctiva and inferior tarsal cartilage (Plate I. fig. 4). It is united to the latter by a short thick process which it gives off in front. In the hollow of the crescent lies the sclerotic; in contact with its lower surface is the sheath of the inferior oblique. At its largest part, which is in close proximity to the conjunctiva, the crescent is at least a tenth of an inch thick, more than twice the bulk of the rest of the capsule of Tenon. This thickening is due to the presence of the suspensory ligament, and it is clear that the data afforded by this examination corroborate the preliminary sketch.

It may interest those who perform operations upon the dead body to know a simple way of demonstrating this ligament. Supposing that the upper jaw has been removed in the ordinary way, it is only requisite to take away a little fat to expose its under surface. If the capsule of Tenon be opened next, by dividing the ocular conjunctiva, a finger may be thrust into its interior and pressed downwards to make the suspensory ligament tense. The band of it which crosses in front of the inferior oblique is especially resistant. But by far the clearest idea of the suspensory ligament may be obtained from horizontal sections, although perhaps this method is slightly artificial. These should be made on a level with the canthi (Plate I. fig. 5). The insertions of the ligament into the malar and lachrymal bones are very distinct; each is about the eighth of an inch thick, and is attached vertically for at least half an inch. They are opposite the equator of the eye, and are about on a level with its lower half. The lowest parts of these bony insertions approach the floor of the orbit. The inner one is fastened to the periosteum which covers the lachrymal crest; in front its fibres pass over the lachrymal sac; behind it is continuous with the periosteum of the orbit and the lowest part of the check ligament of the internal rectus. As the ligament approaches the eye, it spreads out, and is continuous with the capsule of Tenon. The outer insertion of the suspensory ligament adheres to the periosteum of the malar bone just behind the external edge of the orbit, and

at this point its posterior surface receives fibres from the check ligament of the external rectus. It is important to note that its under surface is fastened to the floor of the orbit by numerous irregular fibrous fasciculi; and it is further attached to the orbit through its connections with the sheath of the inferior oblique.

Uses of the Suspensory Ligament.—The most important duty of the suspensory ligament, to support the eye, is obvious. When the eye has been removed from its upper surface, either by an ordinary excision or by taking away the lower half of the globe from a horizontal frozen section, considerable pressure may be made upon the upper surface of the ligament without doing more than stretch it. It is a matter of common observation that immediately after excision of the superior maxilla, the eye maintains its position. The presence of the suspensory ligament offers a ready explanation of this circumstance. The expression "immediately" is used, because at later periods the globe may be drawn out of place by cicatrisation. Another qualification is also needed, for I am informed that when the inner and outer walls of the orbit are very freely taken away during the performance of the operation, the eye may drop so much as to entail its removal. Under these circumstances, the orbital insertions of the suspensory ligaments have been destroyed. And it is to be remembered that this accident is likely to occur whenever incisions are carried above the level of the canthi.

In addition to the function which has just been mentioned, the suspensory ligament seems to perform another, which depends upon its connection with the inferior rectus and inferior tarsal cartilage. I have already shown that this muscle is united by one prolongation to the sheath of the inferior oblique, and by another to the front edge of its aperture in the suspensory ligament, and I must now add that these connections contain so many muscular fibres that practically they are offshoots from the muscle. Authors have laid great stress upon the connection between the inferior rectus and the inferior oblique. Although the fact has not been alluded to before, the front edge of the inferior oblique is united by a long and slender fibrous band to the lower tarsal cartilage and its ligament (fig. 4). By this arrangement the inferior rectus is supposed to be enabled to

depress the lower eyelid and cornea at the same time (Cruveilhier, p. 625; Henle, p. 720). There is no question that, when the rectus is pulled upon, the inferior oblique is drawn further into the orbit, but it is doubtful whether its connection with the eyelid is as efficacious as is thought. The fascia which forms the bond of union is so long and slender that it is not even made tense when the rectus is pulled. The lid is removed in quite a different way. When the muscle is in action, it swings the suspensory ligament backwards, and owing to the intimate union of the latter with the inferior tarsal cartilage, the lid also moves (Plate I. fig. 4). This only partially indicates the importance of the prolongation which unites the depressor muscle to the suspensory ligament. Arguments can hardly be required to show that there must be a limit to this swinging movement of the suspensory ligament, and its range seems to be so limited that it is able to control the contraction of the muscle, and so act as a check ligament. It may be mentioned that this function has been assigned to the lower tarsal ligament (Sappey, p. 108), and to the sheath of the inferior oblique (Cruveilhier, p. 224). The chief objection to these theories seems to be that the structures in question are insufficient for the performance of such an office; for it has just been stated that the other connection of the inferior rectus with the lower tarsal ligament is exceedingly meagre, and also that the sheath of the inferior oblique is so delicate that observers have actually doubted whether it reaches the floor of the orbit.

As far as I have ascertained the presence of the suspensory ligament has been strangely overlooked, although authors have attributed some sort of suspensory action to the capsule of Tenon. Cruveilhier (p. 631) calls it "*aponevrose orbito-oculaire, ou aponevrose d'isolement et de sustentation d'œil*," but it is not clear from subsequent details that this author recognised the suspensory ligament or its orbital attachments. Lenoir says (p. 13) "*the aponeurosis of the muscles of the eye form a ligamentous apparatus which maintains the eye in position*." This statement speaks for itself.

Tenon, in his admirable monograph, clearly indicates the presence of a suspensory apparatus. He says (p. 201), speaking of the capsule—"Arriving at the insertion of the adductor and abductor muscles to the globe of the eye, that is to say, near the conjunctiva, and before applying itself to that membrane, it procures from each side a kind of ligamentous wing (*aile ligamenteuse*) which attaches the globe of the eye to the orbit at the greater or lesser angles. These liga-

mentous wings are formed by the apposition of portions of the tunic which pass one above the other below the globe of the eye." It seems as if this account applies to the relations of parts as seen in transverse sections (Plate I. fig. 3), and Tenon's subsequent statements entirely bear out this view, for he proceeds to say that the ligamentous wings send prolongations forward to the conjunctiva and backwards to the recti (p. 202). In these pages the former were simply considered to be part of the capsule, and the latter the check ligaments. Although the writings of this author have been carefully perused, the fibres which pass beneath the globe, and which actually form the suspensory ligament, seem to have escaped his vigilance. The greater part of his "*ailes ligamenteuse*" seems to consist of its upper fibres seen in transverse section.

The Structure and Interior of the Capsule of Tenon.—The capsule of Tenon, in reality, consists of two very distinct layers; an external, which is tough, matted, and resisting, and an internal, which is soft, loose, and yielding. The former layer only has been mentioned so far, and the expressions "*tunica vaginalis oculi*" (Ferrall) and "*tunica albuginea*" (Malgaigne) which have been applied, accurately indicate its characters. Microscopically it consists of white fibrous and elastic tissue. The inner is made of loose areolar tissue, and completely lines the interior of the tunica vaginalis, surrounding the sclerotic and the intra-capsular portions of the muscles. Bonnet calls it the "*subconjunctival fascia*," and says its presence was pointed out by Guérin and Malgaigne; and although this name has continued in use among surgeons,¹ it is hardly free from ambiguity. In the first place, although a small portion of this loose connective tissue is beneath the ocular conjunctiva, yet the thin anterior part of the capsule of Tenon intervenes between them. And, moreover, the expression scarcely conveys an adequate idea of the extent or appearance of the tunic, which invests not only the front but also the back of the sclerotic. Its close resemblance to the outer covering of blood-vessels, with which everyone is familiar, suggests that in the remainder of this paper it should be called the *tunica adventitia oculi*.²

Vertical and horizontal frozen sections afford the best means of examining the interior of the capsule of Tenon. In these it

¹ Wecker, *Maladies des Yeux*, i. p. 696, Paris, 1868, &c.

² The tunica adventitia is probably the structure involved in capsulitis, (Wecker, p. 697); also Power, *Illustrations of Disease of the Eye*, London, 1867, p. 15.

is quite easy, with a blunt instrument, to separate the sclerotic from the interior of the capsule, and it will be found that the tunica adventitia adheres to the latter but provides a covering for each tendon. These investments are continuous with one another, and unite the contiguous edges of the tendons, but the strength of this union is increased by fasciculi, which the muscles themselves send to the tunic.¹ The connection which is formed in this manner between the superior rectus and superior oblique is so definite that the muscles may be said to form "a loop capable of gliding in the trochlea."² Although adherent to the sclerotic by a definite semi-lunar insertion, the recti usually send fibres to the globe as soon as they touch it; in order, therefore, to hook up the tendons, as in a squint operation, the instrument requires to be carried well back.

The tunica adventitia must be taken away to expose the apertures by which the muscles pierce the capsule of Tenon (tunica vaginalis), and when this is done six openings are brought into view, transmitting, of course, the four recti and two oblique muscles. Each muscle is slightly attached to the margin of its aperture by the tunica adventitia, and when this has been removed, a band of fibres is seen crossing the posterior edge of the opening (*i.e.*, the edge between the muscle and the eye). These ligamentous bands are portrayed in the diagrams as slight thickenings of the capsule (Plate I. figs. 3 and 4).

Since no name has been given to these ligaments, in the ensuing pages they will be called the "intracapsular ligaments." Presumably they constitute the pulleys which Ferrall (p. 338) supposed protected the globe from pressure, but it is clear that many questions demand an answer before this assumption can be allowed to pass unquestioned. It must be proved that they have sufficient strength and immobility to resist the action of the muscles. And when this problem has been solved in a satisfactory manner, it remains to be seen whether their situation is appropriate.

The Intracapsular Ligaments.—In order to expose the intra-

¹ Wecker, ii. 994.

² Cruveilhier, p. 624. This loop is delineated by Lenoir (plate i. fig. 8), and Cruveilhier (pp. 629 and 630) considers that it makes a sort of check ligament for the superior oblique. Merkel, however, attributes this duty to a fascial prolongation which extends from the trochlea to the muscle.

capsular ligaments, all the back of the sclerotic as far as the insertions of the recti should be cut away or dragged forwards. Next, the tunica adventitia should be dissected from the interior of the capsule and from the surface of the tendons. When this has been accomplished, the arrangement of the fibres is distinct and perfectly easy to trace. The openings of the inner and outer recti look like vertical slits in the interior of the capsule, and are situated exactly opposite the equator of the eye, and a vertical band of fibres strengthens the inner (ocular) edge of each (Plate I. figs 3 and 4). If now a small hook be passed beneath the ligaments, *i.e.*, between them and the ocular surface of the tendons, the ligaments will be found to resist attempts to pull them away from the inner and outer walls of the orbit. This may be attributed to the fact that their ends are continuous with the insertions of the suspensory ligament which fastens them to the wall of the orbit. Although easily stretched, they seem to have quite enough strength to resist the action of the muscles. If the hook be pushed well beneath them, quite a strong tug is needed, in a spirit specimen, to cause displacement, and if the globe is drawn away from the capsule of Tenon the recti are bent at the place where they pass over the ligaments. In the recent state they are much more supple and elastic. Thus the intracapsular ligaments are, practically, fibrous loops which hold the tendons of the recti to the walls of the orbit, and, being situated just at the equator of the eye, seem admirably fitted to protect it from pressure. In short, these ligaments have sufficient immobility and strength and a position which enables them to act as pulleys and protect the eye from pressure. With regard to the intracapsular ligaments of the superior and inferior rectus, it has been pointed out already that the depressor muscle pierces the suspensory ligament. When, in order to demonstrate the aperture, the tunica adventitia is removed from the interior of the capsule of Tenon, the transverse fibres of which the ligament consists are brought into view. They cross before and behind the opening, and those which are posterior and above the tendon seem to form an intracapsular ligament. They resist endeavours made with a hook to pull them upwards from the floor of the orbit, and they are situated opposite the equator of the eye. In these respects they are qualified to act as pulleys.

It is probable that the suspensory ligament is held down by its insertions, for, as before stated, they descend towards the floor of the orbit, and perhaps the inferior oblique and its sheath, and the fibrous bands mentioned before (p. 18), may render assistance. The slight swinging movement which can be imparted to the suspensory ligament does not seem sufficient to incapacitate its posterior fibres for the performance of this fresh duty.

The intracapsular ligament which forms a pulley for the superior rectus is of considerable length. Its inner extremity is fastened to the trochlea. It reaches this point by uniting with the sheath which surrounds the reflected tendon of the superior oblique.¹ The outer end seems to be attached to the external wall of the orbit just above the abducens. This ligament, therefore, stretches obliquely across from the roof to the outer wall of the orbit, and it is this arrangement which alters the direction of the superior rectus; for the intracapsular part of this muscle makes a very decided bend inwards towards the nose. In other particulars the intracapsular ligament of the superior rectus resembles all the others.

The anatomy of the opening for the two oblique muscles may be briefly described. That for the superior is a simple circular opening, devoid of ligamentous apparatus. This might have been anticipated if the direction imparted by the trochlea to the reflected tendon be considered. The inferior oblique pierces the suspensory ligament (Plate I. fig. 5). Its aperture is just behind and external to the slit of the inferior rectus, but it is separated from it by the intracapsular ligament, which the suspensory ligament forms for that muscle, and, in addition, by a small oblique band of fibres which cross the upper surface of the suspensory ligament (Plate I. fig. 5). It is not improbable that this corresponds to an intracapsular ligament, and its connections endow it with sufficient immobility.

In concluding the account of these structures, allusion may be made to a function which they possibly perform. Although their attachments to the walls of the orbit have not been specified in very positive terms, this is merely because they have not been traced there as distinct bands. Speaking more particularly of

¹ It is interesting to note that Quain comments upon the strength of the investment of the superior oblique tendon, p. 284.

the internal and external intracapsular ligaments, there seems to be little doubt but that they are firmly fixed above and below each tendon. Clearly this would prevent the muscles following the globe in any movement of rotation, and the arrangement of the tendons and openings of the superior and inferior rectus would assist. In other words, they seem adapted to check the tendency of the oblique muscles to rotate the eye. As far as I can ascertain, the oblique muscles are quite unprovided with check apparatus of any kind; but, seemingly, the intracapsular ligaments are perfectly capacitated by their relations to the recti to act as such.

The interior of the capsule of Tenon has been best described by Bonnet, Ferrall, and Lenoir. These observers expose it from in front by first dividing the ocular conjunctiva and tunica vaginalis, and afterwards the tendons of the muscles and optic nerve. The apertures for the muscles have been described and portrayed by Bonnet, but very inadequately (p. 13, plate i.), and Lenoir doubts the correctness of his observations, and says the openings do not exist. Such a conclusion might easily be arrived at if the inner tunic (tunica adventitia) was ignored. Neither of these writers seem to have been aware of the researches of Ferrall, published in 1841; the same year as Bonnet's work, and nine years before Lenoir's. Speaking of the interior of the capsule, Ferrall (p. 338) says—"In the concavity of this tunic, and about half an inch posterior to its anterior or orbital margin, are to be found six well-defined openings, through which the tendons of the muscles emerge in passing to their insertions into the sclerotic coat, and over which they play, as over pulleys, in their course. The tendons are loosely connected to the edges of the apertures by fine cellular tissue, which opposes no obstacle in their gliding movements." This anatomist says nothing more about the anatomy of these openings, but the accompanying figures seem intended to show that a band of fibres extends along the edge of each.

Specimens which illustrate these observations have been placed in the museum of St Bartholomew's Hospital. It is to be noted that whatever has been said applies to specimens which have been hardened in spirit. There is no question but that in the recent state the various ligaments which surround the eye are very yielding and elastic, and that hardened specimens hardly convey a perfect idea of this, but in other respects the results which they afford appear to be reliable.

EXPLANATION OF PLATE I.

Fig. 1. Tendon of Zinn. E. I. and A., external, inferior, and internal recti. Drawn from a specimen.

Fig. 2. Common tendinous origin of superior (S.), external (E.), and internal (I.) recti. L., root of the lesser wing of the sphenoid, to the front of which it is attached. T., tendon.

Fig. 3. Horizontal section of orbit through the centre of the cornea. L., internal, E., external, attachments of the suspensory and check ligaments (*altes ligamenteuse*, Tenon). A., sheath of adductor, and B., sheath of abductor muscles (the latter making a greater bend). Only the tunica vaginalis is delineated, the tunica adventitia being omitted. The ocular conjunctiva has been dotted in.

Fig. 4. Vertical section. The sheath of the levator palpebræ is dotted in above the superior rectus. The capsule of Tenon is thicker below in the region of the suspensory ligament. I. O., inferior oblique. Only the tunica vaginalis is delineated; the tunica adventitia has been omitted.

Fig. 5. Horizontal section through the orbit at the level of the canthi. L., lachrymal sac. The front aperture is crossed by the suspensory ligament, which is pierced by the inferior rectus and inferior oblique. Drawn from a specimen.

**TWO CASES OF AN ABNORMAL CORONARY ARTERY
OF THE HEART ARISING FROM THE PULMONARY
ARTERY : WITH SOME REMARKS UPON THE EFFECT OF THIS
ANOMALY IN PRODUCING CIRROID DILATATION OF THE
VESSELS. By H. ST JOHN BROOKS, M.B., *Demonstrator of
Anatomy in Trinity College, Dublin.* (PLATE II.)**

DURING the course of the Winter Session, 1884-5, two very remarkable instances of a coronary artery of the heart, springing from the pulmonary artery, occurred in the Practical Anatomy Rooms of this University. The apparent rarity of this abnormality, and the curious effect which it has in producing a cirroid dilatation of the vessels in connection with the anomalous arteries, have induced me to put on record the two cases in question.

In the first case that was discovered, the anomalous coronary artery was a vessel which presented a calibre, corresponding in size to that of a crow-quill. It sprang from the right anterior sinus of Valsalva of the pulmonary artery, and passed downwards upon the infundibulum of the right ventricle, upon which it broke up into branches. These could be traced downwards for some distance upon the cardiac wall, and several of them were observed to anastomose with the branches of the aortic coronary arteries. In addition, however, to its cardiac twigs, others of smaller size could be detected ramifying in the coats of the pulmonary artery. The walls of this abnormal branch of the pulmonary artery were exceedingly thin, and presented characters such as one would expect to find in a vein. On slitting up the pulmonary artery its orifice was observed to be placed in a manner identical to the corresponding openings in the aorta, viz., just immediately above the free margin of the semi-lunar segment of the valve.

A consideration of this case will show that a very interesting question is connected with it? Here are two arteries belonging to the different circulations—the pulmonary and the systemic—
- anastomosing with each other. In these circulations, as is well

known, the arterial pressure is very much greater in the systemic than in the pulmonary; how then did the blood flow in the anomalous coronary artery? There cannot be a doubt that it acted very much after the manner of a vein, and that blood flowed through it towards the pulmonary artery, and from thence into the lungs. The wonderful effect of such a condition on the vessels in connection with the anomalous artery is shown in the second case.

The subject in which the second anomalous coronary artery was found was an elderly male. The vessel had precisely the same origin, viz., from the right anterior sinus of Valsalva, but it was very much larger, presenting a calibre quite equal to that of the aortic coronary arteries, which were in this case of unusually large size, and very atheromatous; as in the preceding case, the origin of this vessel was placed beyond all doubt by slitting up the pulmonary artery and finding the orifice immediately above the corresponding semi-lunar valvular segment. So far as could be made out it gave no branches to the heart, but passed for a short distance to the left, and then entered a complicated mass of tortuous, thin-walled, dilated vessels, not unlike a cirroid aneurism. This arterial mass was placed more or less around the pulmonary artery—lying chiefly behind and to the left of it, whilst a prolongation passed upwards upon the trachea and behind the aortic arch. The arteries composing it were bound together with dense connective tissue, so that it was exceedingly difficult to unravel them. Three large arteries (in addition to the pulmonary branch), entered this curious arterial arrangement. Of these one came from the right aortic coronary artery and passed behind both the aorta and the pulmonary artery to reach its destination, the second was a branch of the left subclavian, and it arose from this vessel in the root of the neck close to the inner margin of the scalenus anticus, and descended in front of the aortic arch and pulmonary artery to take part in the formation of the cirroid mass; the third branch took origin from the posterior aspect of the transverse portion of the aortic arch, and immediately entered the arterial mass. These three channels were of nearly equal size, presenting a calibre rather greater than that of a crow-quill. They are all abnormal branches, and the question comes to be, How

have they sprung into existence. There can be little doubt that the whole arrangement of dilated tortuous vessels has arisen originally from a condition similar to that detailed in the first case, viz., from an anastomosis between a pulmonary and an aortic coronary artery. The double arterial pressure upon the walls of these vessels has led not only to their own dilatation, but has opened up channels which under ordinary circumstances are invisible. These extra channels are probably formed out of certain of the minute arteries which are given off for the supply of the coats of the great vessels. Why the tortuosity and dilatation should have occurred in the one case and not in the other, it is impossible to say. It is likely, however, that the inosculation in the second case had been originally of a more direct and larger kind.

From the cirroid mass several arteries ran upwards upon the trachea and were evidently concerned in the supply of its wall, whilst one was traced into the lung of the right side upon the back of the bronchial tube.

The problem as to how the blood flowed in this arrangement is one of great difficulty. The three systemic arteries (viz., from the aorta, subclavian, and the right coronary) doubtless conveyed the blood into it; in all probability the pulmonary coronary branch acted as the channel by which the blood was drained away. A small quantity of the blood, however, was utilized for the supply of the trachea and the right lung.

W. Krause (quoted by Henle) records a very similar case to the first of those described in this paper. In his case, however, the anomalous branch came from the left anterior sinus of Valsalva of the pulmonary artery.¹

EXPLANATION OF PLATE II.

Fig 1. (1) Branch from right coronary artery, about $\frac{1}{3}$ inch from its origin and passing behind aorta and pulmonary artery (indicated by dotted line); reappears at (2), where it gives off three branches (3), and anastomoses with an anomalous coronary branch (4), which arises from right anterior sinus of Valsalva of the pulmonary artery. From this

¹ *Zeitschr. f. rat. Med.*, 1865, xxiv.

anastomosis two branches ascend in front of the bifurcation of the pulmonary artery and the transverse portion of arch of aorta and join anomalous branch (5) arising from subclavian artery near origin of vertebral.

Fig 2. The three branches (3) ascend, forming a cirroid anastomosis between the pulmonary artery and the trachea, give off (6) a branch to right bronchus and join anomalous branch (7) arising from aorta.

ON A SECOND BURSA CONNECTED WITH THE INSERTION OF THE BICEPS, AND ON SOME RARE ABNORMALITIES. BY A. WARD COLLINS, M.R.C.S., L.R.C.P. Lond., *Assistant Demonstrator of Anatomy, University College, Liverpool.*

THE extreme ease with which the tendon of the biceps (of the arm) plays between the adjacent structures in the movements of pronation and supination might perhaps lead one to imagine the existence of some means, in addition to the bursa usually described, adapted to the free permission of this movement.

I have recently found that there is such an additional means present, in the shape of a second bursa, situated on the inner or ulnar face of the tendon.

This second bursa may be found from the front (after reflection of the superficial muscles and with the radius supinated), in the interval between the oblique ligament and the tubercle of the radius, but can be more readily displayed from behind, after removal of the superficial muscles, by forcibly pronating the radius and reflecting the supinator brevis from the radius inwards.

If an arm, in which the insertion of the biceps is exposed, be placed with the anterior surface upwards, and the radius completely supinated, it will be found that the smooth posterior surface of the tubercle (that is the portion of the tubercle which is continuous with the posterior surface of the rest of the bone) comes as far forward as the point at which the ulna attaches the oblique ligament. Let this be taken as the fixed point, then mark that spot on the tubercle which is opposite this point; now rotate the radius into the position of complete pronation and mark that point on the tendon which is opposite the fixed point. The two marks will be from three quarters of an inch to an inch distant from one another, and it is this portion of the tubercle and tendon included between the marks which is lubricated by

this additional bursa which intervenes between it and the following structures :—

1. The pad of fat filling interval at bend of elbow.
2. The oblique ligament, which separates the bursa from the upper part of the flexor profundus digitorum.
3. The supinator brevis.

The size of this bursa appears usually to be about one inch by three quarters, the long diameter corresponding to the long axis of the tendon.

The first case in which I met with this second bursa was in a very muscular subject, and the thought occurred to me at the time that it might perhaps be an adventitious development consequent upon the unusual muscularity of the individual, but as I have since ascertained its presence in all the other cases (so far, eleven in number) in which I have sought it, I feel fairly justified in assuming it to be a normal structure.

ABNORMALITIES.

The following cases, with one exception, have been observed in the dissecting-room here during the last twelve months. Case IV. occurred more than two years ago, and unfortunately only a very incomplete record was kept of it:—

CASE I. In this case the brachial artery gave off from its upper third a vas aberrans, the destination of which will be subsequently seen, but was otherwise normal, and divided at the usual level.

The ulnar artery was normal, but the radial took the following erratic course (see diagram) successively downwards, outwards, upwards, inwards, and then downwards again, this latter portion passing in front of the first part.

There was thus formed a complete circle of a diameter, sufficient to admit the tip of the little finger, lying upon the lower part of the biceps tendon, and (in the dissected condition) fully exposed in the interval between the supinator longus and the pronator teres.

The upper part of this circle was joined by the vas aberrans already mentioned, and *through* the circle the profunda vein

passed up to join the median cephalic. Immediately after completing the circle the radial gave off its recurrent branch, and was normal in the rest of its course.

CASE II.—The ulnar artery sprang from the brachial opposite the insertion of the coraco-brachialis. Inclining backwards it passed superficially *behind* the internal condyle; in the lower third of the fore-arm it came gradually forwards again over the tendon of the flexor carpi ulnaris, to reach its usual situation on the front of the annular ligament. The common interosseous trunk, in addition to its terminal branches and the ulnar recurrent arteries, gave a small branch, which accompanied the ulnar nerve to within two inches of the wrist.

CASE III.—On the reflection of the rhomboids, by the dissector of the upper extremity, an artery was found perforating the third external intercostal muscle, a little outside the angles of the ribs, and on subsequent dissection the following facts were ascertained:—The transversalis colli artery was continued as the superficial cervical only, and no trace of a posterior scapular could be found, either derived from the thyroid axis or as a direct branch of the subclavian.

The artery which appeared under cover of the rhomboids was derived from the third intercostal, and equalled the usual size of the vessel it replaced—the posterior scapular. After perforating the intercostal muscle, it extended for about two inches in a direction which varied with the position of the scapula, and then turned downwards in the interval between the serratus magnus and the rhomboids, to be distributed like the corresponding part of the posterior scapular artery.

CASE IV.—In this case the popliteal artery, soon after entering the space, divided into two nearly equal trunks, which lay anterior and posterior to another respectively, and reunited after extending separately for two inches. No note was made as to the derivation from these two divisions of the usual branches of the popliteal.

CASE V.—On the right pleural cavity being opened, the apex

of the lung was found to be cleft by a vertical fissure two inches and a half deep, which extended from the inner surface near the anterior border, backwards and onwards to the rounded posterior border, and divided off from the rest of the upper lobe a smaller internal portion, which measured three inches from before back, two and a half from above down, and one inch from side to side.

The upper part of the pleural cavity was divided in a corresponding manner by a double falciform fold of pleura two and a half inches deep, which descended vertically from a point just external to the apex (which was an inch and a half above the clavicle), and divided the dome into two compartments, of which the inner lodged the small portion of lung already described. The free concave lower border of this fold of pleura arched from the right side of the fifth dorsal vertebra behind, to the junction of the second costal cartilage with the sternum in front, the highest point of the arch being on a level with the centre of the manubrium; and in this free border was contained the vena azygos major, the fold of pleura with the contained azygos vein thus presenting a somewhat striking resemblance to the falciform ligament of the liver and the obliterated umbilical vein. In this case, therefore, the vena azygos major, when it reached the fifth dorsal vertebra, instead of arching over the root of the lung to join the superior vena cava, arched across the pleural cavity, contained in a fold of pleura, to the junction of the second costal cartilage with the sternum, where it ended by joining the right innominate vein near its termination, which in this case was at a rather lower level than usual. It received all the intercostal veins from its own side; those from the upper four spaces running between the layers of the pleural fold to empty themselves into it as it lay in the free margin, but had only a small branch of communication, with the vein of the opposite side, across the front of the tenth dorsal vertebra.

On the left side the first intercostal vein joined the vertebral, the remainder emptying themselves into a single left azygos vein, which terminated in the innominate of that side.

ABNORMALITIES OF THE LOBES OF THE HUMAN
LUNG. BY A. ERNEST MAYLARD, B.S. Lond., *Extra
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THE subject of the following few remarks is based upon abnormalities in the lobes of the lung found in three specimens which presented themselves in the course of the usual *post-mortem* examination in the Pathological Department of the Western Infirmary, Glasgow.

Before entering into any discussion upon the subject, it may be as well to briefly describe the specimens.

The first is that of a right lung with no indication of a middle lobe, but the development of a third or accessory one on its inner surface; the second is that of a left lung with a subdivision of the upper lobe; and the third, a right lung with an incomplete separation of the normal middle lobe.

The first specimen came under the notice of Dr Coats while conducting the *post-mortem* of a man who had died from cancer of the bowel. Viewing the lung from the front, it presents all the appearances of a left viscus, with the exception of a slight "puckering" situated on the anterior margin, at the junction of the lower and middle thirds. This looks as if there was some indication of a natural separation of the usual third lobe, but the condition seems to be more likely pathological in its origin. Examining the internal aspect of the lung, a small isolated lobe is seen extending upwards from the root to near the apex. At its attachment below it is about two inches wide, the centre of its bases being immediately over the root of the lung. Roughly, it may be described as tongue shaped, extending to within half an inch of the apex, and being itself about three inches long. The lobe has all the appearance of being an added one, and not a mere separation from, or division of, the normal upper lobe. The remaining two specimens, consisting of both right and left lung, I removed from the body of a man who died from osteomyelitis, following the operation of osteotomy for genu valgum.

The left lung is found to be divided into two lobes by the usual line of intersection; but springing from the anterior margin, at the junction of the two lower fourths, a second fissure is seen extending obliquely upwards, and incompletely dividing the upper lobe into two. This fissure is about two inches long, reaching to within one and a half inches of the main division, and thus detaching a narrow elongated piece of lung, in shape not unlike the lobe described in the above specimen. The right lung of this same case showed, as briefly mentioned above, an incomplete separation of the middle lobe, the natural line of division not extending more than an inch and a half from the main sulcus.

The two main classes into which anatomists have usually divided variations in the number of the lobes of the human lung are—(1) those where the normal number have been lessened, either from actual deficiency of development of the lobes themselves (A.) or of the fissures which normally divide them (B.); and (2) those where the number is increased either by accessory lobes (A.) or by additional fissures cutting off extra ones from the main divisions (B.).

In the first class mentioned (Subdivision A.) the lessening of the number of lobes from failures of development appears to be extremely rare. The state of atelectasis cannot be accepted as coming under this head, since the condition is not one where there is absence of development of lung tissue, but where failure of normal expansion is the sole cause of what is only an apparent deficiency. Ponfic, in Virchow's *Archiv*, vol. 1. p. 633, however, has recorded a case which rightly belongs to this class. The right bronchus was developed, and found to be connected with an ovoid body five lines long, three and a half broad, and two and a half thick, imbedded in a reddish-yellow gelatinous tissue, which filled the right half of the thorax. In the Subdivision (B.) of the same class, where the number of lobes is lessened from non- or incomplete development of the normal fissures, the frequency of illustrative cases varies. Thus the complete absences of any division of either the right or left lung is extremely rare, if, indeed, it has ever been found, although homology¹ would lead one to believe the condition possible. Vesalius (*De Corp. hum. fabr.*, libr. vi.) speaks of the human lungs being

¹ The Orang has two lungs, each existing as a unique lobe.

non-lobed, but Sappey seems to doubt somewhat this, believing rather that modern pathology would have revealed interlobar adhesions, the result of a pleurisy, as the cause of the apparent mono-lobed condition. The right lung of the first case narrated above would seem to belong properly to this class, inasmuch as but for the accessory lobe on the inner aspect the organ would really be bilobed from the absence of the normal separation of the middle lobe. There certainly was, so far as one could judge, nothing of the nature of adhesions, which had obliterated a previously existing fissure. Nevertheless, one must allow that a pleurisy occurring anterior to birth might possibly lead to an adhesion between two lobes which subsequent development might fail to disconnect. This, however, without other indications, is unlikely.

Of cases where normal lobes exist, but incompletely detached examples are numerous enough, and the right lobe of the third case is an example in point.

In Subdivision A. of Class II., where there is development of accessory lobes, numerous cases have been recorded, almost all, however, illustrations of two particular conditions affecting the right lung; one where an accessory lobe has been found above the root of the old lung, and the other where it appeared to occupy a similar position below it. In the latter condition, the peculiar constancy of the relations of the lobe, and the resemblance it holds to a similar one normally existing in quadrupeds, has caused it to receive a special name. Thus, in virtue of Darwin's theory, it has been called by Pozzi an *anomalie reversive*; by other anatomists the *azygos lobe*; the *lobus impar* of Owen, the *lobus accessoire* of Duvernoy. Such a position, therefore, for an accessory lobe seems a well-recognised one.¹ Not so, apparently, with the other class of cases, where the lobe is found below the root of the lung. In recent years four such cases appear to have been reported, and, as these all occurred about the same time, it would lead one to believe that the anomaly may not be so rare after all. Professor Chiene published one such case in the *Journal of Anatomy and*

¹ See also cases described by Dr E. W. Collins in *Trans. Royal Irish Academy*, 1874; by Dr Laurence Humphry in this *Journal*, July 1885; and by Dr Edwards in the *American Journal of the Medical Sciences*, July 1885.

Physiology, vol. iv. p. 89. In every respect as to size, shape, and position it resembles the one described above. Shortly after the record of Professor Chiene's case, Professor Cleland followed with the narration of a precisely similar one in the same volume of this *Journal*, p. 200. A little later Wenzel Gruber recorded two similar cases (*Bull. de l'acad. Imp. des. Sc. de St Petersburg*, 5 Ap. 1870). In all these four specimens it was noticed that the vena azygos major passed around the base of the supernumerary lobe. Unfortunately, in the usual comparatively rough method of removing the lungs at a *post-mortem* as contrasted with a careful dissection in the anatomy room, the relation of the azygos vein to the lobe was not observed. If, however, Professor Cleland's explanation of the abnormality (as suggested at the conclusion of his own case) be correct, it is extremely probable that the vein did pass over it as in other cases, for the existence of the lobe is made to depend upon the course of the vein constricting or notching a piece of the upper lobe, which at an early period had become adherent to the thoracic wall. This explanation tends to class these cases rather with those where an extra lobe is due to the subdivision of a primary lobe than to the development of an additional one, as was originally supposed.

In Subdivision B, where the number of lobes is increased by the fissuring of the primary ones, examples are frequently met with, and the abnormality is probably one of the commonest. The second case narrated above is an illustration of this, the extra lobe being formed at the expense of the normal left upper one. A specimen almost identical with one here described was shown at the Société Anatomique in Paris some years back, and is to be found depicted in Cruveilhier's *Traité d'Anatomie descriptive*, vol. ii. p. 282, 5th edition.

The cases of more than four lobes to the right and three to the left must be very rare; and although most writers upon the subject allude to their having been observed, it is generally with a kind of reserve, as if the statement were one of those literary innovations, doubtful as to its origin, which, once having gained admission to publication, had become handed down by subsequent writers until it assumed the appearance, and finally received the acknowledgment, of being a fact. There is a condition, however, of pulmonary division alluded to by

Cruveilhier which might possibly have led to this belief in a multiplicity of lobes. Thus Cruveilhier states :—" Il n'est pas rare de voir la base du poumon divisée en plusieurs lobules presque complètement séparés du reste du poumon, auquel ils ne tiennent que par un pédicule, dans lequel on trouve toujours un canal aérien, une artère et une veine pulmonaires."

THE NATURE OF LIGAMENTS. (PART IV.) By J. BLAND
SUTTON, F.R.C.S., *Lecturer on Comparative Anatomy,*
Middlesex Hospital Medical College. (PLATE III.)

DURING the past few months I have enjoyed the opportunity of dissecting some very interesting animals: this new material has enabled me not only to continue my inquiry into the "nature of ligaments" but has supplied me with additional facts in support of my views on this subject, and led me to see the mode of origin of others of these structures, whose nature was certainly not very obvious when I first took up the matter. The ligaments I propose dealing with in this paper are:—

1. The inter-articular fibro-cartilages of the knee-joint.
2. The bicipital loop in the thigh of birds.
3. The gleno-humeral ligament.
4. Certain ligaments in the wrist and carpus.
5. The anterior annular ligaments of the ankle-joint, and the inter-articular cartilage in the medio-tarsal joint of birds.
6. Rudimentary toes in birds.
7. Certain ligaments in the vertebral column, particularly the posterior common ligament; also the relation between the subnotochordal rod and the anterior common ligament of the spine.

The Inter-articular Fibro-cartilages of the Knee-Joint.

On a previous occasion I not only attempted to show that the inter-articular fibro-cartilages of the knee-joint of man were metamorphosed tendons, but even ventured to associate the inner one with the semimembranosus and the outer one with the popliteus muscle. Evidence has gradually accumulated in later dissections, which supports my view in regard to the origin of these fibro-cartilages, and the knee-joint of Iguana will be chosen, for it is interesting beyond measure in its bearing on the question. In this form, as well as in some other reptiles, we find a very remarkable muscle in the thigh, known as the

femoro-caudal. It is an exceedingly large muscle, and arises from the infero-lateral aspect of the caudal vertebræ: it is inserted by a large, broad, and strong tendon into the base of the trochanter on its extensor aspect. A little space before its insertion this tendon gives off, at right angles to its lower border, a long, thin, and delicate one, which passes down the thigh, on the inner side of the great sciatic nerve, to the popliteal region, where it passes between the fibula and tibia to blend with the outer part of the inter-articular fibro-cartilage of the knee-joint.

The appearance of the muscle and tendon is shown in Plate III. fig. 1, as well as the inter-articular fibro-cartilages of the knee-joint, which may be thus described:—The outer fibro-cartilage presents itself as a circular disc, concave above, convex below, in fact a true meniscus; the concavity on the upper surface is for the reception of the external condyle of the femur. To the posterior part of the disc, the long tendon connected with the femoro-caudal muscle blends. Attached to the outer side of the meniscus is a smaller disc, which is subservient to the head of the fibula, for in this form, as in so many of the Sauropsida, the head of the fibula plays on the outer femoral condyle, and in this particular instance a fibro-cartilage is interposed, as in the case of the tibia and femur. The inner cartilage, which is firmly connected with the outer one so that the two forms a continuous plate of fibro-cartilage, is fairly circular in outline, and presents a round hole in the middle. To the posterior border is attached the semi-membranosus muscle, and two or three others, which for the most part have no representatives, at least as individual muscles, in man. On the anterior aspect, this fibro-cartilaginous disc is firmly attached to the capsule of the joint, thereby differing from the corresponding cartilages in man and mammals generally, in whom the semilunar cartilages are not only distinct from each other but directly attached to the head of the tibia, as well as being connected by the coronary ligaments to the margin of the articular surface of the head of the tibia. The preceding facts show indubitably, that, in lizards at least, the inter-articular fibro-cartilages are the modified tendons of muscles which have become inter-articular during the modifications the joint has passed through in its evolution; the details of the probable mode

by which it has been brought about were detailed in a previous paper (in vol. xix. of this *Journal*, p. 253).

In *Iguana* it is very obvious that other muscles beside the semimembranosus must be held responsible for the inner fibro-cartilage, and that the popliteus muscle has nothing to do with the outer one, for the muscle in question arises from the tibial aspect of the head of the fibula, and is inserted into the posterior surface of the upper half of the tibia. Hence it is rendered in the highest degree probable, that in those mammals in whom the popliteal tendon becomes attached to the outer semilunar fibro-cartilage, the fusion is secondary.

In the face of these facts, it seems to me that the following conclusions are warranted by the evidence:—

1. The semilunar fibro-cartilages of the knee-joint result from the metamorphosis of muscles and tendons.
2. There are no particular muscles with which they can be with certainty associated in mammals, except in part at least, the semimembranosus.

The curious characters of the long tendon of the femoro-caudal incited me to look deeper into its nature. I have assured myself of its existence in the same condition as it is figured on Plate III. fig. 1, in *Iguana tuberculata*, *Sphenodon*, *Hatteria punctata*, the Stump-tailed Lizard, *Trachydosaurus rugosus*, a Monitor, *Monitor niloticus*, *Phrynosoma coronatum*, *Chamæleon*, *Chamæleon vulgaris*, and several others.

Although in these forms the tendon belongs to the femoro-caudal, nevertheless careful dissection, especially in *Sphenodon*, convinces me that this fusion is secondary. In *Menobanchus*, as in other urodele batrachians, there exists a muscular mass on the ventral aspect of the femoro-caudal, also arising from the caudal vertebra, and blending with the muscular stratum which flexes the pes as in the act of swimming. In the lizards the chief portion of this muscle is represented by the tendinous portion of the femoro-caudal. As lizards are certainly not in the habit of constantly using their hind-limbs for the purposes of swimming, and as the muscle in question is rendered to a certain extent inoperative by being nipped between the tibia and femur, I assume that, being only of use passively, it became metamorphosed into tendon, the proximal portion of which

became utilised by the femoro-caudal, which formed an alliance with it. As this tendon is so constant an element in the thigh of lizards, it was necessary to trace, if possible, its subsequent history in higher forms. It seems to me that this link is supplied in the Crocodilia.

In the thigh of a young Alligator (*Alligator mississippiensis*), the following arrangement exists:—The tendon, as shown in Plate III. fig. 2, arises as usual from the femoro-caudal, but, instead of an insertion into the inter-articular cartilages of the knee, it has acquired an attachment to the outer head of the gastrocnemius muscle. In higher forms it entirely disappears. Here we have a very interesting example of the gradual loss of a muscle (due to change in the mode of life of animals), whose history we are able to trace from its original functional condition in an aquatic creature, its tendinous existence in semi-aquatic forms, and its total disappearance in those animals which are purely terrestrial. Similar instances of muscles furnished with long and thin tendons will be mentioned further on, as occurring in birds and mammals, but their history is not quite so clear and convincing as is the case with the reptilian femoro-caudal.

The Bicipital Loop in the Thigh of Birds.

Let any one take the trouble to dissect the thigh of a fowl from the outer side, then a most interesting arrangement of myological structures will reward his labour, but the one to which especial attention is invited is the singular tendinous loop which transmits the tendon of the biceps muscle and a branch of the great sciatic nerve.

On reflecting the skin, the most superficial muscle is the *tensor fasciæ* or *gluteus primus* as it is termed by some. If this muscle be turned up, or removed, the deep muscles will be exposed; the most conspicuous is the biceps, which has the following attachments:—It arises from the upper three-fourths of the post-acetabular ridge (a slight bony elevation which separates the post-acetabular area from the external lateral surface of the ischium). Just in front of the *tensor fasciæ* the fibres converge to form a rounded tendon, which on the outer side of the popliteal region is bent sharply downwards by passing through a tendinous sling or loop; it is inserted nearly half

way down the fibula to a bony prominence on its outer side. The loop in question is attached to the lower end of the femur; the outer limb is slightly connected with the head of the gastrocnemius, which is situated to its outer side. A nerve to the leg and foot, derived from the great sciatic, accompanies the tendon through this sling (Plate III. fig. 3). This tendinous loop, studied in the fowl and similar birds, is curious and puzzling, but I shall here endeavour to show, or at least adduce evidence in support of the view, that it is derived from the metamorphosis of the muscular fibres of the outer head of the gastrocnemius muscle. Before doing so, however, it will be necessary to state that the muscle, here termed biceps, has not the same anatomical relationship as the muscle so named in the leg of mammals, indeed, to my mind it is certainly not homologous with that structure, and as there is little utility in discussing the morphology of muscles in so highly specialised a form as that of the fowl, as compared with man, I do not propose to waste time on this matter. In the thigh of the Rhea (*Rhea americana*), the Emu (*Dromæus novæ-hollandiæ*), *Ramphastós loco*, and in many other avian forms, this loop through which the biceps tendon passes is modified in this way:—"The inner limb is a tendon of great strength and of considerable thickness, but the outer limb of the loop is constituted by the muscular and tendinous fibres of that head of the gastrocnemius muscle which is attached to the external femoral condyle; hence one half of the loop is tendinous, the other muscular (Plate III. fig. 4). This arrangement clearly affords the clue by which we may seek to interpret the origin of so singular a pulley, for clearly it is the result of the metamorphosis of muscle fibres.

Being fortunate enough to obtain for anatomical purposes a good specimen of *Iguana tuberculata*, my first efforts were at once directed towards the muscles of the thigh.

If the dissection be commenced from the outer side, as in the bird, a prominent muscle, referred to by Mivart as the *ilio-peroneal*, is easily recognised. It has the following attachments and relations:—It arises from the posterior part of the outer side of the ilium, covered by the posterior portion of the tendinous origin of the gluteus maximus, and even a little overlapped by the gluteus medius. It is inserted by a strong tendon,

which dips between a muscle called *peroneus primus* by Mivart, and the outer head of the gastrocnemius, into the outer side of the fibula near its summit.¹

It will be necessary, before discussing the ilio-peroneal muscle, to take into consideration the muscles named *peroneus primus* and the gastrocnemius. The first muscle arises by a strong tendon from the summit of the outer side of the external condyle of the femur. It becomes tendinous below the outer malleolus; a portion of this expansion gains an insertion into the peroneal border of the fifth metatarsal bone, a little above its middle. On the posterior aspect of the ankle-joint it expands into a broad ligamentous aponeurosis, and joins with the expansion of the gastrocnemius.

The gastrocnemius consists of two distinct parts; one arises from the internal condyle of the femur, and has a slight attachment to the head of the tibia near the insertion of the semimembranosus and semitendinosus. Passing downwards it becomes aponeurotic near the ankle-joint, and blends with a broad tract of tissue—the plantar fascia. The second portion arises from the femur, just above the external condyle; passing down the leg it becomes aponeurotic near the ankle-joint, and blends with the plantar fascia.

In very many birds the gastrocnemius arises by three heads, an inner one from the tendon of the rectus, and cnemial crest of the tibia; the middle head from between the condyles of the femur, and an outer one arising from the external condyle of that bone. Between these two heads—the middle and the external—passes the biceps tendon.

On comparing the fowl's leg muscles with those of Iguana, it becomes evident that the muscle marked *peroneus primus* in the Iguana is really the equivalent of the outer head of the fowl's gastrocnemius, and that the bird's biceps cruris is really the representative of the ilio-peroneal of the Iguana; they agree in position and especially in their relation to the great sciatic nerve.

Admitting this to be so it will give us the steps or stages by which the bicipital sling has become fashioned. They may be briefly summarised as follows:—

¹ Mivart's admirable account of the "*Myology of Iguana tuberculata*" (*Proc. Zool. Soc.*, 1867) has been to me of the utmost utility in my dissections.

1. In its original condition the so-called biceps passed between two muscles; it matters little whether we call it outer head of gastrocnemius or peroneus primus.
2. The two muscles tend to fuse near the knee-joint, and enclose the distal end of the biceps.
3. The leg becomes bent at a more or less acute angle with the thigh; this leads the biceps to drag on the muscle-fibres of the gastrocnemius through which it passes. The muscular tissue in relation with the tendon of the biceps thus plays a passive part, and becomes metamorphosed into tendon.
4. The inner head first separates from the parent muscle; the outer head may do so and form a complete tendinous sling; differentiation may not proceed so far, the outer head remaining in many birds permanently attached to the outer portion of the gastrocnemius.

The question at once arises, Have the facts any bearing on the myology of the mammalian limb? My answer is this. If the biceps cruris in man be carefully traced, the insertion is not by any means confined to the head of the fibula, but its fibres spread into a broad aponeurotic expansion covering the outer side of the leg. The relative size of the biceps in man, as Mivart points out, is much inferior to its possible development. In some forms, *e.g.*, the Agouti (*Dasyprocta agouti*), the muscle combines with the tensor fasciæ and gluteus maximus to form an almost continuous sheet of muscle, extending from the pelvis over the outer side of the leg to the ankle-joint. I was very much interested in the biceps of a Rhinoceros, in whom the muscle, after being inserted into the fibula, was prolonged by means of an enormously thick and broad tendon to the ankle-joint. This and similar facts induces me to venture the following explanation. The muscle in Iguana called peroneus primus, that in birds known as outer head of gastrocnemius, the broad muscular expansion in the Agouti, the enormous tendon of the Rhinoceros, and the broad fibrous expansion in man, must all be regarded morphologically as one and the same structure.

If one compare the limbs of a lizard or a bird with that of man or any of the higher mammals, he will be struck with the fact that in the latter forms the muscles are invested by strong

aponeuroses known as the deep fascia, and separated one from the other by fibrous intermuscular septa. Not so in the Sauropsida (Birds, Lizards, Crocodiles).

Careful inquiry, by means of dissection, will force an impartial worker, in the end, to the conclusion that the deep fasciæ and the intermuscular septa are in reality the result of the metamorphosis and regression of muscular tissue, at least so far as the fore and hind-limbs of most mammals are concerned.

Other loops for the transmission of the tendons of muscles are not unknown, for example, the pulley which transmits the tendon of the superior oblique muscle in the orbit of man; and the loop which holds down the tendon of the extensor longus digitorum muscle in the foot of many mammals and birds. These will be considered subsequently; but the only tendinous sling which in any way approaches the bird's bicipital loop, is one attached to the scapula of a few birds, and which transmits the tendons of the latissimus dorsi muscle. It is represented in the elaborate memoir, "On the Anatomy of the Spheniscidæ," by Prof. Morrison Watson (*Challenger Reports*, part xviii. plate x. fig. 4, vol. xvii.). In the Penguins the latissimus dorsi muscle consists of two distinct portions, which end in two tendons, and are slung up to the neck of the scapula by a fibrous pulley. Having recently had an opportunity of dissecting a Black-footed Penguin (*Spheniscus demersus*), I feel convinced that this loop may be regarded as metamorphosed fibres of the deltoid muscle.

The great point of interest in connection with the bicipital loop is the fact that it is an exclusively avian character, at least so far as recent forms are concerned, and that with very few exceptions, among them the Steganopod (*Phætho*), no known bird lacks the bicipital sling.

Before leaving birds it may be interesting to briefly note one or two special features in relation to the wing, which will go to strengthen the view of the metamorphosis of muscles into tendons.

Allusion has been made in a previous paper¹ to the interesting and extreme examples of muscular degradation presented in the fore-arm and manus of the various species of

¹ This *Journal*, vol. xviii. p. 235.

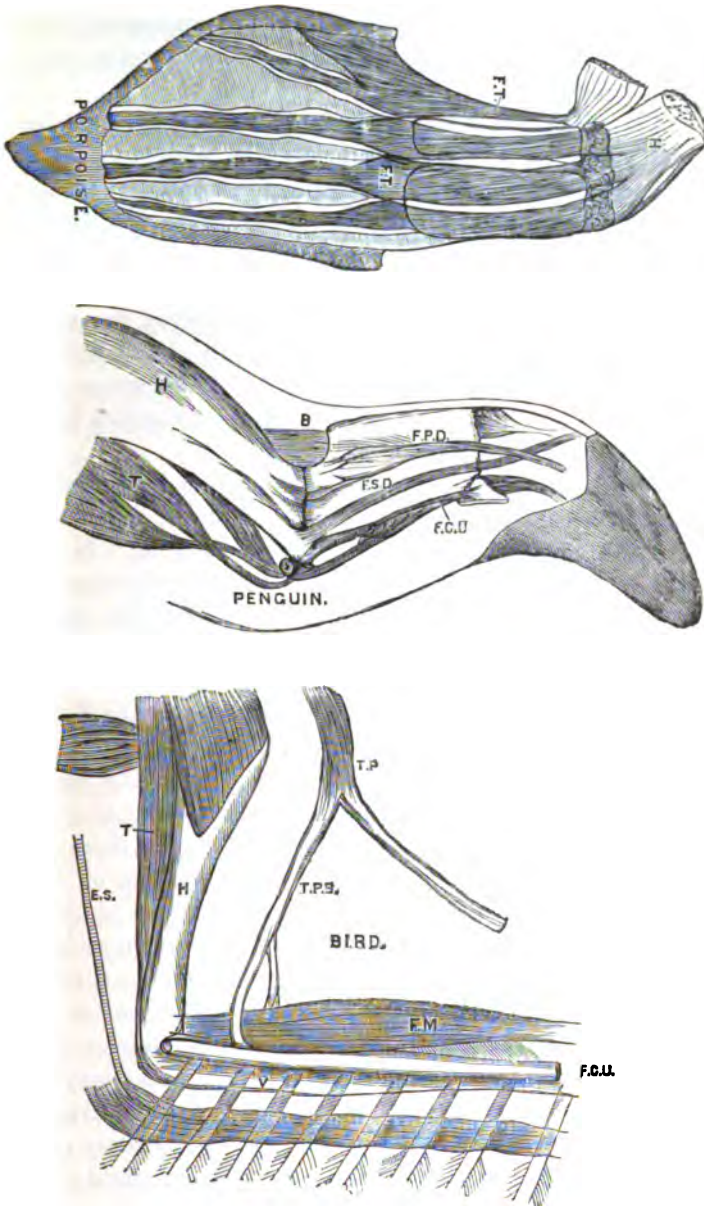


FIG. 1.—Three figures to show degeneration of muscles in the manus of the Porpoise and the wing of a Penguin. The lower wing is for comparison. H., humerus; F.T., fibrous tissue; T., triceps; F.P.D., flex. prof. digitorum; F.S.D., flexor sublimis digitorum; F.C.U., flexor carpi ulnaris; T.P., tensor patagii; E.C., expansor secundariorum; F.M., flexor muscles.

Cetacea, especially the Narwhal (*Monodon monoceros*), and the Porpoise (fig. 1). The wings of Penguins afford good instances of a similar process.

If Prof. Morrison Watson's elaborate "Report on the Spheniscidæ" collected by H.M.S. 'Challenger,' be referred to, it will be readily seen that the flexor profundus, flexor sublimis digitorum, and flexor carpi ulnaris muscles are represented by strands of fibrous tissue, whilst in those muscles of the fore-arm which are represented by contractile tissue it is so small in amount, that the structures in question are hardly worthy the name of muscles when compared with the fore-limb of the flying bird (fig. 3). It affords an admirable example of the wings used as paddles losing their intrinsic muscles and becoming like unto the fore-limbs of a Porpoise.

The wing represented in fig. 3 is intended principally to show the usual condition of muscles in birds, so as to offer favourable comparison with the Penguin's wing. It shows, however, a peculiarity worth pointing out; for instance, in this bird, as in one or two others I have examined with regard to this matter, the flexor carpi ulnaris muscle is not present as a muscle, but as a thick, strong, and elastic tendon (F.C.U.). Thus whilst it illustrates the amount of degradation in the Penguin's wing, it bears amongst its muscles an early example of that process. This condition is seen in the wing of the Secretary Vulture, the Rail (*Rallus aquaticus*), Razor Bill (*Alca torda*), and others. Whilst dealing with the bird's wing, there is one other muscle worthy of mention. Every student of human anatomy must have experienced a certain amount of curiosity when he dissects for the first time the plantaris muscle; this strange structure sinks into insignificance when compared with the celebrated ambiens of the bird's leg, or the tendon of the femoro-caudal in the Lacertilia. Of all strange muscles, the one known as the expansor secundariorum muscle in the bird's wing stands pre-eminent (Plate III. fig. 5). It is a small triangular muscle arising from the quills of the last few secondary remiges at the elbow. Its remarkably long and slender tendon, which frequently traverses a fibrous pulley on the axillary margin of the *teres* muscle, runs up the arm side by side with the axillary vessels and nerves, to be inserted in the thorax into the middle

of a tendon which runs from the inner side of the middle of the scapular element of the scapulo-coracoid articulation, to near the middle of the thoracic border of the sterno-coracoid articulation, at right angles to it when the fore-limb is extended.

In the ducks and geese among the *Anseres* the tendons under consideration, when they enter the thorax, run towards one another and join, after having expanded out, in the middle line in front of the oesophagus, and behind the trachea.

Not the least interesting feature in this muscle is the importance Garrod attached to it for the aid it afforded him in his *Classification of Birds*. For all that relates to this extraordinary muscle, I must refer the reader to Garrod's memoirs:— "On the Anatomy of *Chauna derbiana*" (*Proc. Zool. Soc.*, 1876), "The Anatomy of Passerine Birds" (*ibid.*, 1874, 1877, and 1878), and to the volume of his *Collected Scientific Papers*, 1881.

The Gleno-Humeral Ligament.

In this *Journal* (vol. xix. page 32) I made an attempt to prove that the gleno-humeral band or ligament, present in the shoulder-joint of man, may be regarded as the divorced tendon of the subclavius muscle. Certain facts and arguments were set forth in support of this view. Since that time no opportunity has been lost of testing the point, and at the present time I feel more convinced that it is true, my dissections having extended over a very wide range of animal forms.

When I first took up the subject the only gleno-humeral band known to me, besides that of man, was the structure so commonly referred to as "the ligamentum teres in the shoulder-joint of the frog." It seemed to me that, if the view as to the origin of this curious band were the correct one, a gleno-humeral ligament ought to be present with tolerable frequency, especially as the subclavius muscle is so constant in mammals and in other forms above the fishes. To this end I have examined every available animal that has come under observation for the past year. When writing the second part of these papers I was able to make allusion to five mammals, in whom a perfect ligament existed in the shoulder-joint; in the third part I was able to add seven mammals to the list, and at the present date

the list has grown so large that it will be possible to make a few general statements concerning it.

Hoping that other anatomists may be induced to look into the matter, a list is appended of those forms in whom I have found the ligament, not as a mere thread or thickened piece of capsule, but as a strong discrete ligament, often rivalling the long tendon of the biceps in size, and presenting itself inside the joint as freely as the ligamentum teres in the cotyloid cavity.

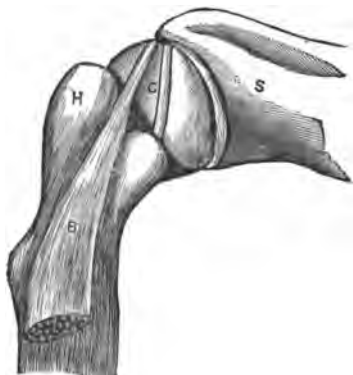


FIG. 2.—The shoulder-joint of a Beaver (*Castor canadensis*), to show the large size of (G) the gleno-humeral ligament; S, scapula; H, humerus; B, biceps.

The accompanying woodcut (fig. 2) shows the gleno-humeral ligament in its usual condition, and as such it existed in all the forms enumerated in the accompanying list:—

· QUADRUMANA.—*Cercopithecus cynosurus*, 8;¹ *C. lalandii*, 7; *C. callitrichus*, 2. *Macacus sinicus*, 20; *M. cynomologus*, 10; *M. nemestrinus*, 6. *Theropithecus gelada*. *Cynocephalus hamadryas*; *Cyn. anubis*, 2. *Chrysothrix sciurea*, 5. *Cebus fatuellus*; *Ceb. capucinus*, 3; *Ceb. albifrons*. *Ateles paniscus*; *A. ater*, 2. *Hapale jacchus*, 4; *H. penicillata*, 2. *Cercocebus albigena* (in this species the ligament is thin).

LEMURIDÆ.—*Lemur catta*, 3. *Galago alleni*, 3; *G. maholi*, 2. *Perodicticus potto*, 2. *Chirogaleus coquereli*. *Microcebus smithi*. In *Chiromys madagascarensis* it was present but very thin. The ligament is absent in *Galeopithecus* and *Nycticebus tardigradus*.

INSECTIVORA.—*Talpa europea*, 3. *Erinaceus europæus*. *Tupaia peguana*, 2. *Centetes madagascarensis*. *Microgale longicauda*. *Sorex vulgaris*.

RODENTIA.—*Pteromys magnificus*. *Arctomys monax*. *Cynomys*

¹ The figure always refers to the number of specimens examined in regard to this particular question.

ludovicianus, 3. *Castor canadensis*, 8. *Myoxus glis*; *M. dryas*. *Fiber zibathicus*. *Dipus aegypticus*; *D. hirtipes*. *Myopotamus coypus*, 6. *Hystrix cristata*. *Erethizon dorsatus*. *Sphingurus prehensilis*. *Calogenys paca*. *Dasyprocta agouti*. *Sciurus hypopyrrhus*. *Xerus getulus*. *Sciuropterus fimbriatus*. *Gerbillus indicus*. *Cricetomys gambianus*. *Mus barbarus*. *Rhizomys badius*. *Octodon cumingi*. *Cerodon rupestris*. *Arvicola amphibius*. *Mus musculus*; *Mus decumanus*. *Lepus cuniculus*.

In some rodents the ligament is very large, and occupies a groove in the cartilage covering the head of the humerus.

MARSUPIALIA.—*Didelphys cancrivora*; *D. virginiana*, 2; *D. opossum*; *D. philander*, 2; *D. viverrina*. *Phalangista vulpina*, 3. *Hypsiprymnus gaimardi*. *Phascolomys wombat*. *Cuscus maculatus*, 2. *Belideus breviceps*.

EDENTATA.—*Chlamyphorus truncatus*.

The gleno-humeral ligament is *absent* in the mammals mentioned in the lists which follow, but in many a thickened band was detected in the capsule which may have represented it.

QUADRUMANA.—Chimpanzee (*Anthropopithecus troglodytes*), 3. Orang-outang (*Simia satyrus*), 2. Gibbon (*Hylobates leuciscus*), 2. *Macacus inuus* (in this form a thick band may be seen in the capsule).

CHIROPTERA.—*Pteropus poliocephalus*. *Desmodus rufous*. *Plecotus auritus*.

HYRACEE.—*Hyrax capensis*, 2.

I dissected a Hyrax within a few days of examining the joints of a Rhinoceros, and the similarity of the hip-joint in the two forms was very striking. The Hyrax, like the Rhinoceros, has no ligamentum teres in the hip-joint. This seems to have been overlooked by previous observers.

UNGULATA.—Rhinoceros (*Rhinoceros sumatrensis*). *Tapirus americanus*. *Equus*. *Bos taurus*; *B. indicus*. *Oreas canna*. *Llama huanacos*; *L. peruana*. *Sus scrofa*. *Porcula salvania*. *Babirussa alfurus*. *Strepsiceros kudde*. *Capra hircus*. *Ovis aries*; *O. blandfordi*; *O. burrhel*. *Moschus moschiferus*. *Tragulus*, species incerta. *Hydropotes inermis*. *Muntjac sclateri*. *Hippopotamus amphibius*.

CETACEA.—*Phocaena communis*.

CARNIVORA.—*Felis leo*; *F. tigris*. *Canis familiaris*. *Herpestes ichneumon*; *H. griseus*. *Lycan pictus*. *Lutra vulgaris*. *Nasua rufa*. *Phoca vitulina*. *Enhydra marina*, 2. The Common Cat. *Felis javanensis*, 2.

Very many other species of Carnivora and Ungulata have been examined with a negative result, but at first I did not make note of these cases, therefore, the species cannot be indi-

cated individually. This defect I hope soon to remedy, especially as the two groups are abundantly represented in the Zoological Society's menagerie.

Although in most of the Carnivora the gleno-humeral ligament is absent, yet it turns up in that singular form the Two-spotted Paradoxure (*Nandinia binotatta*); it is also present in the Himalayan Bear (*Ursus tibetanus*).

EDENTATA.—*Bradypus tridactylus*, 3. *Tatusia peba*; *T. hybrida*; *T. sexcinctus*; *T. villosus*. *Myrmecophaga jubata*, 2. *Tamandua tetradactyla*, 2. *Manis didactyla*, 2. *Orycteropus capensis*.

In the two specimens of the Pangolin (*Manis didactyla*) the hip-joint lacked a ligamentum teres.

MARSUPIALIA.—*Perameles lagotis*. *Phascolarctos cinereus*, 3. *Macropus rufus*; *M. giganticus*; *M. melanops*. *Halmaturus bennettii*; *H. ualabatus*; *H. derbianus*.

MONOTREMATA.—*Echidna hystrix*. *Ornithorhynchus paradoxus*.

The following animals do not possess a ligamentum teres in the hip-joint:—the Seal, Elephant, Rhinoceros, Walrus, Ornithorhynchus, Echidna, Sea-otter (*Enhydra marina*) (of this form I have had the good fortune to dissect the joints in two specimens), Sloth, Orang, Walrus, *Hyrax*, and *Pangolin*.¹

Lastly, the following rules may be of interest:—

1. Every mammal in whom I have up to the present found a gleno-humeral ligament likewise possesses a ligamentum teres in the hip,
2. Those mammals in whom a ligamentum teres is absent in the hip also lack a gleno-humeral band.
3. Those forms in whom the gleno-humeral is well developed, the ligamentum teres in the hip is also very thick and strong.

The reasons for regarding the gleno-humeral ligament (or gleno-humeral band when it merely appears as a thickening in the capsule) as the divorced tendon of the subclavius muscle may be briefly enumerated.

¹ The mammals whose names occur in the lists came under observation at the Zoological Society's Gardens,—most of them recent, others preserved in the Prosector's room,—and I am indebted to Mr F. E. Beddard for opportunities of examining them. A few others are from the stores of the Royal College of Surgeons, London. See "On Ligamentum Teres" Mr Savory's paper in *Jour. of Anat. and Phys.* vol. viii. p. 291.

1. All Amphibians which possess the equivalent of the subclavius—the *epicoraco-humeral* of Mivart—in a well-developed form, lack the gleno-humeral ligament.
2. Birds in whom the subclavius muscle, under the name of *levator humeri*, reaches its maximum of development, passes through the shoulder-joint as a tendon to be inserted into the humerus, no gleno-humeral ligament exists.
3. In mammals the subclavius is a very constant muscle, and a gleno-humeral ligament exists in a very large number of them; when not represented as a free ligament it may often be detected blended with the capsule of the shoulder-joint, but lying *between* it and the synovial membrane.

Certain Ligaments of the Wrist and Carpus.

As our mother earth receives alike the remains of kings, philosophers, and peasants, so Nature buries in fibrous tissue structures which were in histological rank far superior to the ligamentous tissue which now hides them, so disguising their former nature and true significance that they become reduced to the level of structures whose duty is menial indeed.

Morphological problems of the greatest interest may centre around a single band of fibrous tissue, whilst in the immediate neighbourhood ligaments abound of functional value, but of no interest to the morphologist.

The ligaments of the wrist and carpal-joint are excellent witnesses as to the truth of this statement. The drawing (Plate III. fig 6) shows the appearance of the carpus and wrist of man in frontal section.

The ligament, dignified with an asterisk, passing from the angle of the scaphoid to the os magnum is only of occasional occurrence, and deemed so insignificant that very few text-books of anatomy deign to consider or figure the little band.

For a clear understanding of the true meaning of this ligament we must descend to that most generalised form of carpus, or typical carpus,—that presented by the Water Tortoise (*Chelydra serpentina*),—as seen in Gegenbaur's well-known figure. The carpus consists of two principal rows, a proximal containing

three bones, a *radiale*, *os intermedium*, and *ulnare*; the distal row is made up of five bones, called *carpalia*, and numbered respectively 1, 2, 3, 4, and 5, commencing from the radial side. Wedged between the two rows is a single bone,—the *os centrale*.

This “*os centrale*” exists in the carpus of a very great number of animal forms; it occurs in Amphibia, Reptilia, and Mammalia, even persisting as a normal element in the carpus of the Orang and Gibbon.

The bone attracted considerable attention when Henke, Reyher, and Rosenberg drew attention to its temporary existence in the human carpus. Rosenberg showed that the *os centrale* may be detected as a cartilage nodule in the carpus of a human embryo at the second month of intra-uterine life; it is well marked during the third, but disappears during the fourth month of embryonic life. The matter has become additionally interesting from the fact that Professors Wenzel Gruber¹ and Turner² have placed on record instances of the occurrence of the *os centrale* in the carpus of adult human individuals. Being greatly interested in the question, I examined by dissection, and by means of sections prepared for the microscope, a very large number of foetal hands. The existence of the rudimentary cartilage in the position of the *os centrale*, as described by Rosenberg and Kölliker, admits of no doubt whatever, and I have come to the conclusion that the ligament, indicated by the asterisk in Plate III. fig. 6, is the remains of that cartilage nodule, for whenever the cartilage nodule representing the *os centrale* is present the ligament cannot be detected, but in many cases, by no means in all, the spot previously occupied by the cartilage is filled up by fibrous tissue, which may persist through life, but in the largest number of instances disappears entirely.

Professor Leboucq of Gand published a paper in the *Arch. de Biologie*, tom. v., 1884, entitled “*Recherches sur la Morphologie du Carpe chez les Mammiferes*,” which contains a detailed account of an investigation into the development of the carpus. Sixty-eight hands, furnished by forty-five foetuses, were examined,

¹ Wenzel Gruber, *Archiv. Anat. Phys.*, 1869, p. 331; also, *Beobacht. aus der Mensch. und Vergleich Anatomie*, Heft iv., Berlin, 1883.

² Turner, *Jour. of Anat. and Phys.*, vol. xvii. p. 246.

varying in age from the second to the fifth month of intra-uterine life. This anatomist comes to the conclusion that the os centrale of the carpus does not atrophy, as Rosenberg has stated, but fuses with the scaphoid. Leboucq had previously expressed a similar view, in a paper published in the *Bull. de l'Acad. royale des Sciences de Belgique*, 3^e series, t. iv., No. 8, 1882.

There can be no doubt of the temporary existence of an os centrale in early foetal life, but opinions are divided as to its fate; probably it is liable to considerable variation in this respect.

The triangular fibro-cartilage of the wrist-joint has been made the subject of some interesting investigations by Professor Leboucq, also contained in the paper "On the Morphology of the Carpus" before referred to. This observer finds that in the human foetus, from the third to the fourth month, there exists in this structure a small elliptical cartilaginous nodule, which at this period of development is in close relation with the pisiform bone. Until quite recently it has been customary to regard the pisiform as a sesamoid bone developed in the tendon of the flexor carpi ulnaris muscle. Recently, owing mainly to the comparative researches of Gegenbaur and Wiedersheim, doubts have been thrown over this view of its nature. According to Leboucq, the cartilage for the pisiform appears before the tendon of the flexor carpi ulnaris, therefore it cannot be a sesamoid. He then points out that the mode of development of the inter-articular fibro-cartilage and the pisiform ossicle induce him to believe that these two structures are part of a complex apparatus, of which the pisiform bone is a separate portion. Leboucq also figures the carpus of a Gibbon (*Hylobates leuciscus*) preserved in the Museum of the University of Gand, in which there is a cartilage nodule occupying the position of the inter-articular fibro-cartilage and articulating by its distal end with the pisiform bone; this inter-articular nodule he believes represents the temporary cartilage nodule in the human foetus. The temporary existence of this cartilage is a fact of considerable interest, but whether it justifies the remarkable explanations contained in Leboucq's paper, requires further investigation, but it justifies its introduction here in connection with the subject of the nature of ligaments.

The Anterior Annular Ligaments of the Ankle-Joint.

Finding that so many of the ligaments of the human body had yielded interesting results to my cross-questioning, I made an endeavour to ascertain, if possible, the nature of the anterior annular ligaments of the ankle-joint. Although my labour has not enabled me to see, in the clearest light, the true meaning of these structures, nevertheless the results are in no small degree interesting, and are worth detailing.

The first fact which strikes one, on looking carefully into the arrangement of the annular ligaments, is that the upper and lower ligament, frequently described as parts of one structure, are really quite distinct the one from the other. This will be readily seen on looking into the anatomy of the parts as exhibited in the Cebine Monkey (*Cebus albifrons*), where they present the most generalised mammalian condition.

It is necessary to caution the reader against accepting the *exceedingly loose* and unsatisfactory descriptions of these ligaments current in most of the anatomical text-books. The figures are as grotesque as the descriptions when compared with the dissected parts. The best account is afforded by Quain's *Anatomy*, 9th edition.

The following account will answer for man, with one slight exception, which will be noted in due course:—

In the majority of Primates, as in *Cebus albifrons*, which is chosen for description, the superior anterior annular ligament is a broad strong band of fibrous tissue, passing anteriorly to the extensor tendons, and attached on either side to the margins of the tibia and fibula, as shown in Plate III. fig. 7. The tibialis anticus muscle is not provided with so distinct a tunnel in the ligament as is the case in man.

The inferior ligament is really a fibrous loop attached to the os calcis by its two extremities, which are in contact where they arise from the bone, so that they form an exceedingly narrow loop, which just admits of the passage of the extensor longus digitorum tendon, as shown in the figure; from the inner limb of the pulley a fibrous cord passes beneath the extensor proprius hallucis and tibialis anticus muscles, to be

attached to the internal malleolus, blending with the tibial attachment of the superior ligament as shown in fig. 3.

By studying the relations of this structure in a large number of mammalian forms, it turns out that the loop which encircles the extensor longus digitorum is the essential portion of the ligament, but that the fibrous cord passing to the internal malleolus is entirely secondary, and exhibits extreme vagary in the way it disports itself with regard to the extensor hallucis and tibialis anticus muscles.

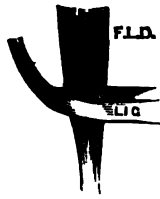


FIG. 3.—The inferior anterior annular ligament of the ankle-joint of a Monkey. F. L. D., extensor longus digitorum muscle.

I find it impossible to deal satisfactorily with the annular ligament of the ankle-joint, without taking into consideration the condition these ligaments present in birds, and as the inquiry has led me deeply into the subject of the development of the tarsus in the feathered tribe, and certain facts of some interest have come under notice, it will be necessary to go systematically into the matter.

The Avian Tarsus and Annular Ligaments.

The tibia, or more correctly the *tibio-tarsus*, of a bird is a bone very characteristic of this class. It is a cylindrical bone, usually about half as long again as the femur. The proximal extremity presents two somewhat concave articular surfaces for the femoral condyles; in front it is produced into a prominent cnemial crest or process, which in a few cases (*Struthio* and *Rhea*) is ossified as an epiphysis. In the *Dinosauria* this process may be variously subdivided. The distal end of the bone is terminated by a trochlear or pulley-like articular surface. Not unfrequently there is an oblique bar of bone on the anterior face, just above the trochlea; this osseous loop transmits some of the extensor tendons (fig. 4). The true composition of this bone will be

considered when treating of its development. The fibula of birds is usually imperfect, and presents itself as a slender osseous rod attached to the outer side of the tibio-tarsus. Its proximal end articulates with the outer condyle of the femur being received in the fibular fossa; the distal end gradually undergoes diminution and fuses with the tibio-tarsus. Although as a rule the fibula is shorter in the adult bird than the tibia, yet it may be of the same length as in some of the Penguins.

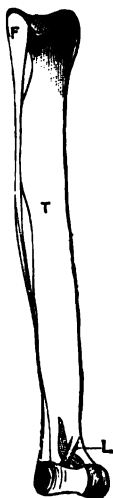


FIG. 4.—The tibia and fibula of an Eagle, to show the small size of the fibula.
L, the osseous loop for the extensor longus digitorum.

The segment beyond the tibio-tarsus is a compound of certain bones of the tarsus and the metatarsus, hence it may be correctly referred to as the tarso-metatarsus; the various metatarsals which compose it fuse together to form a single bone.

As the proximal part of the tarsus becomes confluent with the tibia, and the distal portion fuses with the metatarsus, it thus comes about that the joint between the tibio-tarsus and the tarso-metatarsus is in fact a mesotarsal articulation really corresponding to the medio-tarsal joint of man, which exists between the os calcis and astragalus as its proximal elements, and the scaphoid and cuboid bones as the distal bones.

The above statements are warranted by an appeal to the development of the parts in birds. Gegenbaur (*Untersuchungen zur*

Vergleichenden Anatomie der Wirbelthiere, Erstes Heft, "Carpus und Tarsus") proved that the distal end of the tibia, which in the young bird is separated from the main bone by a suture, is not an epiphysis, for the cartilage in which it ossifies is separate; this individuality in the cartilaginous state distinguishes it as an element, an epiphysis being a distinct ossification in a continuous cartilage.

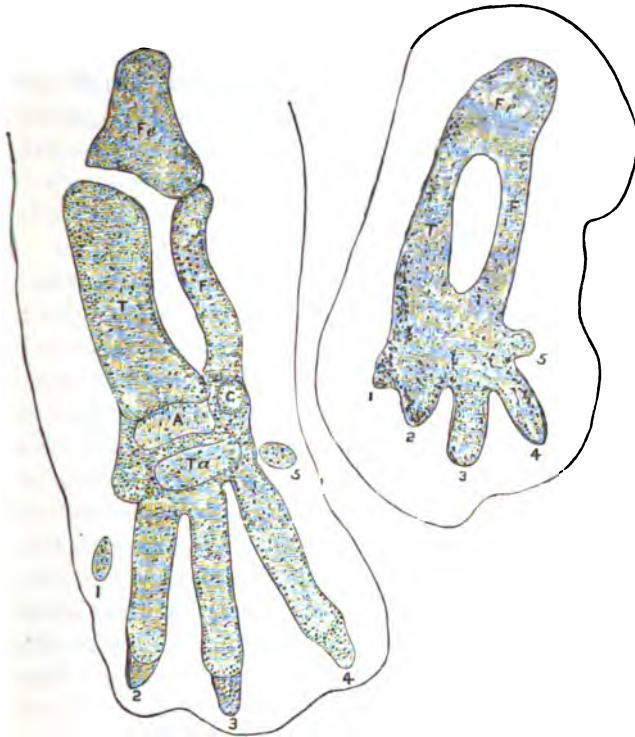


FIG. 5.—The leg of a Chick at the fifth day of incubation. The leg of a Chick at the eighth day of incubation (after Johnson). Fe., femur; T., tibia; F., fibula; A., astragalus (tibiale); C., os calcis (fibulare); Ta., tarsalia. The numerals refer to the digits.

In order that the true nature of the parts shall be correctly comprehended, it will be safer to give in brief outline the development of the bird's leg, which has been worked out by Gegenbaur, Rosenberg, Baur, and Miss Johnson.¹

¹ "Development of the Pelvic Girdle in the Chick," *Quart. Jour. Mic. Science*, vol. xxiii. (This paper contains numerous references to the literature of the subject.)

In the limb of a chick, five days old, the tissue is condensed axially into a single mass, and the skeleton of the limb is produced by the subsequent elongation and segmentation of the mass.

On the sixth day the limbs present the condition represented in fig. 5. All the chief elements may be recognised, though they are completely continuous. The tarsus is continuous with the tibia and fibula above and with the metatarsals below. Five metatarsals are present.

At the eighth day all the elements of the tarsus are at their most distinct and independent stage, though they are still united with one another, with the tibia and fibula, and with the metatarsals, by the condensed tissue of the groundwork of the tarsus (fig. 5).

Later, the distal and proximal parts of the tarsus become separated, and the two proximal elements fuse together. Next, the proximal parts fuse with the tibia, which has grown more than the fibula, so that the latter no longer reaches the tarsus. The posterior lower edge of the tibia first becomes continuous with the proximal tarsal cartilage, while the anterior face of the latter gives off an upward process, the so-called "ascending process of the astragalus," which fits into a groove in the tibia, and remains for a long time separate from it. At about the same time the distal part of the tarsus fuses with the metatarsals, first with the second, next with the fourth, and lastly with the third. All these processes take place while the tarsus is still cartilaginous. In the chick two ossific nuclei later make their appearance in the proximal piece of cartilage, the inner one representing the astragalus, the outer and smaller piece the os calcis. The distal piece of cartilage represents the tarsalia.

In the majority of birds the astragalus sends up a long osseous "spike," which fits into a groove on the anterior surface of the tibia, as shown in Plate III. fig. 10, and is commonly referred to as the ascending process of the astragalus. This spike has been shown by Morse¹ to have an independent ossific centre, and he considers it to correspond with the intermedium bone of the typical tarsus. The question is one so full of interest, and as I wish to give an account of some observations of my own on the subject, it is well to refer in some detail to Morse's paper.

¹ *Anniversary Memoirs of the Boston Society of Nat. History*, 1880. Morse *On the Identity of the so-called Ascending Process of the Astragalus with the Intermedium*.

It appears that Professor Wyman sent a note to Morse, to the effect that he had found in the tarsus of an embryo Heron, a long style-shaped bone, broadest at its distal extremity, lying in front of and at the distal end of the tibia, which he believed to represent the so-called ascending process of the astragalus, but which had an independent centre of ossification, and remained free from the other tarsal bones until the young had left the egg. Morse has previously shown that, as the proximal series of bones become united, the fibula diminishes in size proportionally with the rapid increase of the tibia, becoming finally a splint-like bone with its attenuated distal end far removed from the tarsus; the tibia, on the contrary, enlarges, so that its distal extremity equals in transverse diameter the two proximal tarsal bones.

The intermedium, while occupying its proper position between the tibiale and fibulare, and finally uniting with them, becomes displaced, so to speak, by standing in front of the tibia. As proving the correctness of this assumption, it may be mentioned that the bone may be found occupying its true position in the tarsal series, and between the distal extremity of the tibia and fibula in the embryos of those birds in whom it is represented.

An examination of the tarsus in the embryos of the Tern (*Sterna hirundo*), Petrel (*Procellaria pelagica*), Sea Pigeon (*Uría grylle*), Eider Duck (*Somateria mollessima*), Herring Gull (*Larus argentatus*), and in the Great Auk (*Aptenodytes pennanti*), showed that in these birds the intermedium is present as a separate bone. It lies at first in a line with the proximal row of tarsal bones, opposite the space between the tibia and fibula. As the tibiale and fibulare coalesce the intermedium is crowded upwards and outwards so as to occupy a position in front of the tibia. It is the last bone to unite with the confluent tibiale and fibulare.

Since reading Morse's paper, I have had an opportunity of investigating the condition of the ascending process of the astragalus in a Cygnet of *Cygnus mutis*, and in an Ostrich chick. In the Cygnet the "bony spike" was present as a separate ossification, exactly as Morse figures it. In the case of Struthio the process was just in the act of uniting with the astragalus; on making a longitudinal section through the lower end of the tibio-tarsus the line of separation was clearly visible. These two

cases clearly confirm the existence of the ascending process as an independent ossicle.

I felt it was absolutely necessary to enter minutely into the details of the ossification of the bird's tarsus for two reasons:— (1) To show that the bony bridge on the lower end of the tibio-tarsus is an "adventitious" ossification, (2) to prove its relationship with the tarsus—these two conditions being essential to establish its identity with the inferior annular ligament of the mammalian ankle-joint.

In order to show that a great deal of misconception prevails as to the real nature of the oblique bar of bone, I will make the following extract from Mr Parker's paper, "On the Osteology of *Balaeniceps rex*" (*Trans. Zool. Soc.*, vol. iv.):—"The inferior or distal end of the tibia is developed from a distinct osseous centre in young birds, which piece forms all the articular parts and sends upwards a wedge-shaped process in front, the seat of the ossification which makes the large, wide, oblique, tendon-like bridge."

Morse finds that this oblique tendon-like bridge in the Heron and many other birds has no relation with the intermedium, and I am convinced, from the examination of a very large number of birds, that the pulley in question is really the homologue of the loop which in mammals binds down the tendon of the extensor longus digitorum, and has its main attachment to the proximal row of tarsal bones. It is, therefore, an adventitious ossification and not an intrinsic element of the tarsus.

It may be worthy to mention, that, when "hunting" for ossific centres in delicate tissues, one should not be content with carefully examining the parts when moist, for it has happened to me *many* times, when unable to find a nucleus in a recent specimen, the nuclei have become distinctly visible when the parts have been allowed to dry. This need not spoil the specimen, for on soaking cartilage in water it quickly reassumes its plump condition.

So far as the anterior annular ligaments of the bird's leg is concerned, it must be clear to any one who has followed the preceding account that the two structures differ very considerably in their mode of origin as well as in their relation. It must also be very evident that the upper ligament, which

involves all the extensor tendons, is the homologue of the superior ligament at the mammalian ankle-joint, but the deep or inferior loop, ossified in some birds, which transmits the extensor longus digitorum tendon, is the avian representative of the loop attached to the os calcis in most mammals, including man. It may perhaps be advisable to state that the fact of its often undergoing ossification in birds is no objection to its being considered as the homologue of a purely fibrous (and, so far as one knows, always so in mammals) structure, for in the West African Lemur (*Perodicticus potto*) the anterior annular ligament of the wrist-joint (which arises as the result of regression of certain portions of the short muscles of the hand) contains an osseous nodule, thus completing a bony tunnel for the flexor tendons, comparable in a certain measure to the osseous loop at the lower end of the bird's tibio-tarsus.

Admitting then that the ligaments in the legs of birds and mammals are homologous, it necessarily follows that the question be asked, How do these structures arise, and what is their nature?

On extending our view to reptiles and amphibians, we are surprised to find that these forms (or, to be guarded, none of the examples which have been dissected by me) possess annular ligaments at the ankle in any way similar to those we have been considering. In fact, these ligaments might be cited as characteristics of mammals and birds. It thus comes to be very clear that some change in the mode of life or position of limb is responsible for the change. The story of the origin of these ligaments, as I would write it, from the facts revealed by dissection, observation, and reflection on the writings of others, would run thus:—

At the outset it is important to bear in mind the fundamental condition of the limb. In the first stage, a flat muscular sheet passed from the trunk to the toes, lacking segmentation; next, as joints arise in the axis of the limb, the muscular sheet suffered transverse division, many of the muscles destined for the pes taking their fixed point from the femur, the majority of those acting on the leg remaining attached to the pelvis, the tailed batrachian *Menobranchus* bearing excellent testimony on this head.

The extensor muscles in the leg of such forms as Iguana and Chameleon present us with another example of this process, which is extremely valuable in connection with the subject under consideration.

In these forms the extensor longus digitorum arises from the outer condyle of the femur, and slightly from the tibia; it passes downwards, to be inserted—in Iguana, by two tendons into the dorsal aspect and proximal end of the second and third metatarsals; in Parson's Chameleon¹ it goes into the distal extremity of the third metatarsal bone.

The short extensors of the toes are very curious, amounting to eight or nine in Parson's Chameleon. They take origin from quite the lower end of the tibia and fibula, the tarsal ossicle, and metatarsal bones, there being much variation in different forms. In that the short extensors arise from the dorsum of the feet, these forms are in common with mammals, but the mammalian extensor brevis digitorum muscle gained the dorsum of the tarsus by migration, and is thus altogether a secondary condition. In the case of Iguana the short extensors lie on the dorsal aspect of the foot as a result of the primary segmentation.

It is easy to see that in the case of *Menobranchus*, as Gadow has so well shown, the limb was used simply as a paddle whose axis was nearly straight. In the case of Iguana we have to deal with a crawling, creeping, or running creature, whose terrestrial life necessitated the bending of the limb at various angles. This flexion has caused the extensor longus digitorum to secede from the short extensors of the phalanges and to form an attachment to the metatarsus; the distal elements adhering to the fibula, tibia, or any vantage point offered by the tarsus become short extensors.

Subsequently this arrangement became changed as the animal's habits underwent modification, for active movements led to more acute flexion of the foot on the leg, leading to a secondary fusion of the long and short extensors of the foot, whereby its action became continued to the phalanges, but those fibres, by means of which the short extensor was originally attached to the tarsus, become metamorphosed to form an annular ligament or loop for the now compound long extensor of the digits.

¹ Mivart, "Myology of Parson's Chameleon," *Proc. Zool. Soc.*, 1870.

This additional flexion of the foot caused the remaining extensor muscles to exert tension on the connective immediately covering the muscles; this extra tension at a definite spot had the effect of causing a thickening in the tissue, which is recognised as the superior anterior annular ligament.

Hence a comparative study of these two ligaments leads one to the conviction that the mode of origin is different in the two cases; the one being a remnant of a muscular attachment, the other condensed connective tissue, the result of continued strain.

There is yet one other ligament at the medio-tarsal articulation worthy consideration. In the Ostrich, Rhea, and Emu the posterior part of the joint is occupied by a well-developed inter-articular fibro-cartilage of considerable dimensions. It is wedge-shaped, the thin end projecting into the joint, whilst the base is visible posteriorly, filling in an irregular interval between the tibio-tarsus and the tarso-metatarsus. On Plate III. fig. 12 it is represented in position in the leg of an Emu (*Dromæus novæ-hollandiæ*), whilst in fig. 13 it is shown of natural size; the two strap-like ligaments attached to either corner are attached to the margins of the tarso-metatarsus, and serve to keep it in position.

The ligament presents itself in the most complete form in the Ostrich, Rhea, and Emu, but it is present in varying degrees in the medio-tarsal articulation of every bird that I have dissected.

Its constant presence in this situation leads me to suspect that we have in this cartilage to deal with a modified tarsal element, but as young struthious birds are not easily obtained I have been unable to verify my view as to the real nature of this structure. My chief object in mentioning the cartilage is to draw attention to its constant presence, which seems to have escaped the notice of anatomists.

Rudimentary Toes of Birds.

In a short but interesting paper "On the Variations from the Normal Structure of the Foot in Birds,"¹ Mr W. A. Forbes states that the ordinary number of the toes in birds is four, represent-

¹ *Ibis*, 1882, p. 386-390, and in the Memorial Volume of Collected Papers, p. 440.

ing the first, second, third, and fourth digits of the normal penta-dactyle feet. A number of birds are, however, three-toed, the reduction in nearly all cases being effected by the suppression of the hallux. It is not always, however, the hallux that is thus absent in tridactyle birds. In the Kingfishers, of the genera *Ceyx* and *Alcyon*, the foot is three-toed, but the hallux is well developed; the second digit, on the other hand, is reduced to its basal phalanx, thus appearing externally as a mere wart-like eminence on the side of the digit next to it, in a way very similar to that exhibited by some Edentata, in which the fifth digit of the manus is greatly reduced. In the curious passerine genus *Chloronis*, on the other hand, which is also said to be three-toed, the reduction is brought about by the absorption of the most external or *fourth* digit. In the Ostrich, finally, only two digits are present, both the first and second having entirely disappeared.

Whilst engaged dissecting the leg of a young Emu (*Dromæus novæ-hollandiæ*), a stout fibrous band was detected passing from that portion of the tibio-tarsus which represents the astragalus, and gradually becoming indistinct as it descended on the metatarsus. It had no connection with the external ligament of the joint, and lay completely to its inner side. This band is represented in Plate III. fig. 14.

On finding this ligament my suspicion was aroused that I had in this fibrous cord some rudiment of more than common interest, and upon reading Forbes's paper the suspicion became strengthened. Further testimony came to hand, for in a previous paper, "On the Rudimentary Hallux of Birds,"¹ Forbes writes as follows:—"Whilst engaged in working out my Report on the Anatomy of the Petrels for the Voyage of H.M.S. 'Challenger,' I happened to come across Dr Kidder's note on the existence of a rudimentary hallux in *Phæbæria fuliginosa*, a bird hitherto supposed, like other Albatrosses, to lack the hind toe altogether." Forbes not only succeeded in verifying Kidder's observation, but found it present in three other species of Albatrosses that he had in the flesh (*Diomedea exulans*, *D. brachyura*, and *Thalassiarche culminata*). In all these cases the hallux was present in a rudimentary condition, con-

¹ *Proc. Zool. Soc.*, 1882, pp. 548, 549; and in *Collected Papers*, p. 359.

sisting of a small nodule of bone lying beneath the skin in the subcutaneous fibrous tissue, and only appearing externally as a minute pimple-like elevation with no claw.

The discovery of this rudimentary hallux in the *Diomedea* induced Forbes to look for it in other birds, and he succeeded in finding it in certain genera of Woodpeckers (*Picoides* and *Troglodytes*), the hallux consisting of a normal number of phalanges, and of a metatarsal, but all of minute size. The "great toe" thus formed lies completely under the skin, and is only discernible on reflecting the skin carefully.

In many birds possessing the hallux, the union with the tarso-metatarsus is usually brought about by means of fibrous tissue, for whilst the remaining digits articulate directly with the distal end of the tarso-metatarsus, yet in very many instances the metatarsal bone corresponding to the hallux is a very diminutive structure, and the portion corresponding to the shaft is represented by fibrous tissue. In the face of these facts it seems probable that the long fibrous band figured in the Emu represents an aborted hallux. The bird was only two years old.

Similar conditions of the metatarsals and metacarpals may be studied in the Ungulates, especially the Deer. Very many of these animals possess only rudiments of the lateral metatarsals, sometimes only of the distal ends; at other times the distal and proximal ends persist, whilst the intervening portion or shaft exists only as a fibrous tissue. Sir Victor Brooke, in an interesting paper "On the Genus *Cervulus*" (*Proc. Zool. Soc.*, 1874), has given an account of the two paths by which the reduction of the metacarpals has been effected.

I have entered fully into the details of this curious and gradual disappearance of toes from a bony condition into a fibrous tract, not only from its own intrinsic interest but also for the undeniable support it gives to several instances of this curious metamorphosis about the shoulder-joint of man.

So, too, in the case of the bird's fibula, before mentioned as being of equal length with the tibia, but that later its lower end grows at a less rate than the tibia, and eventually the lower end becomes simply represented by a thin band of fibrous tissue.

Some two years ago I was fortunate enough to procure the

fœtus of a young Shetland Pony at about the mid stage of gestation. On dissecting the leg I was surprised to find the fibula not represented by bone, but by a thin, rounded, dense cord of fibrous tissue. Normally in the horse the distal end of the fibula is represented by fibrous tissue, but in this particular case the metamorphosis had extended beyond the usual limits, and had involved the entire bone.

The hands of Spider Monkeys furnish similar instances. These monkeys normally possess four digits, the pollex being usually absent. Occasionally, however, a rudimentary pollex may be detected, and in one instance I found in *Ateles paniscus* a thumb an inch long. In examples of *Ateles ater* the thumb is represented by a band of fibrous tissue arising from a small fibro-cartilaginous nodule on the outer side of the second metacarpal. The nodule in question forms part of the attachment of the extensor ossis metacarpi pollicis tendon.

Many other instances could be adduced of this process of substitution if it were necessary, but I think the instances described above are quite sufficient to establish the fact, that in the limbs as well as in the trunk very important osseous elements may be represented by fibrous tissue.

The Ligaments of the Spinal Column.

On two previous occasions I have attempted to deal with some of the ligaments which unite the various segments of the vertebral column to one another, as well as those which pass from the spine to the skull, or to the ribs and pelvis. Some of these, such as the interspinous and intertransverse, are clearly the remains of muscles; others, such as the ligamenta subflava and portions of the intervertebral discs, have a higher morphological significance, whilst two remarkable ligaments, the anterior and posterior common, remain to be dealt with.

The first real attempt to attach a morphological value to a spinal ligament was that of Rathke, in his famous *Entwicklung der Schildkröten*, 1848, where, in a masterly piece of anatomical reasoning, he shows most conclusively that the os odontoideum of the Turtle, is really the representative of the body of the atlas, and that the ligamentum suspensorium, a thin fibrous band

passing from that process to the margin of the foramen magnum, is the remains of the notochordal sheath.

Rathke had previously promulgated this doctrine in his *Entwicklungsgeschichte der Natter*, so far as the odontoid process is concerned. Cuvier, in his *Recherches sur les ossements fossiles*, had previously identified the true homology of this bone by a study of its condition in the Turtle and in the Matamata Terrapin. Bergmann confirmed the statements of Rathke, and now the matter rests beyond all disputation after the investigations made into the subject as regards mammals by J. Müller, Robin, and Hasse. Then, the fact that the nucleus pulposus in the middle of the intervertebral discs is the remains, in part, of the notochord, lend additional interest to the matter. It is a curious fact that, though in adult mammals we find only a definite ligamentum suspensorium attached to the odontoid process, yet in birds, as Jäger¹ has shown in *Das Wirbelkörpergelenk der Vögel*, we find a suspensory ligament in many other parts of the column. In its most typical form the arrangement may be thus described:—

Between the centra of contiguous vertebræ is a fibro-cartilaginous ring, which is continued inwards in the form of a disc which has free anterior and posterior faces, this portion is called the meniscus; this thins towards the centre, which is always occupied by a hole. The meniscus, when perfect, divides the space between the centra of the opposed vertebra into two synovial cavities. The central perforation in the meniscus is traversed by a ligament, which in the chick contains the remains of the intervertebral portion of the notochord. The shape of the discs and the aperture for the suspensory ligament is shown in Plate III. fig. 15. In some instances the meniscus is reduced to a mere rudiment, in other cases it is united with vertebral bodies, whilst in the caudal region, in its relation to the bodies of the vertebræ, it resembles an ordinary intervertebral disc.

There seems to be no rule by which one could predict the presence or absence of this disc. In two specimens of *Rhea* (*Rhea americana*) dissected by me, the discs and suspensory ligaments were absent, the vertebral centra coming into direct apposition. In the Emu the meniscus is alone represented,

¹ *Sitzungsberichte der Wiener Akademie*, 1858.

whilst in the Pigeon, Fowl, and similar birds the meniscus and suspensory ligaments are present in a perfect condition; when carefully dissected, the neck vertebræ and their discs, alternating and threaded as it were by the suspensory ligaments, present a striking appearance.

If the cervical vertebræ of a child be macerated until the intervertebral discs drop away, it will be found that the vertebral bodies will in many cases remain attached to each notochord; in thickened sheath surrounding the remains of the other by the this way it strikingly resembles the avian suspensory ligament.

It should be mentioned that, in those birds which lack a suspensory ligament between their vertebra, but in whom the meniscus is developed, a small dimple may be often detected in the middle of the articular surface of the vertebra.

The Posterior Common Ligament.—Lying on the posterior surfaces of the bodies of the vertebræ, and extending from the upper surface of the basi-occipital bone to the lower end of the sacrum, is a fairly broad fibrous band. The upper part of the ligament, that which lies between the occipital bone and the axis, is often designated the posterior occipito-axial ligament. The most important features of the posterior common ligament are these:—In the neck it extends quite across the bodies of the vertebræ, in the thoracic and lumbar regions it is broader opposite the intervertebral discs than at the middle of the bodies of the vertebræ: between these narrower portions and the vertebral centra is some loose connective tissue and a venous plexus; so that the ligament is only connected with the spine at the intervertebral discs and the corresponding margins of the vertebræ, presenting throughout its course a series of attached and unattached segments. In this *Journal* (vol. xviii. p. 225) attention was directed to the ligament originally described by Mayer and by Cleland, which in many mammals unites the heads of the ribs of opposite sides, by passing across the dorsal aspect of an intervertebral disc; this ligament, known as lig. conjugale costarum, is present in the foetus of man about the time of birth, but later it unites with the intervertebral disc. An attempt was then made to prove that the ligamentum transversum and ~~the~~ check ligaments of the occipital bone were really persistent

examples of the ligamentum conjugale. Previously Rathke had endeavoured to show that they were simply thickened bands of connective tissue, that observer not being aware of the existence of the remarkable ligament in question. So frequent is the existence of the lig. conjugale in mammals, that the view which would regard the transverse and check ligaments as being of this nature, becomes almost a certainty.

Aided by these facts and a careful examination of the posterior common ligament, the conclusion is irresistible that it must be regarded as consisting of a series of short bands passing from one disc or conjugale ligament to another, merely as a thickened band of connective tissue and of no morphological significance. It should perhaps be mentioned that Bergmann regarded the transverse ligament of the atlas as a thickened portion of the sheath of the notochord. Rathke showed this to be erroneous, for in the Turtle and Coluber the transverse ligament of the atlas exists, whilst the entire thickness of the notochord and its sheath lie in the body of that vertebra—the future os odontoideum,—and that the notochordal sheath and transverse ligament can be clearly seen distinct from each other.

The anterior common ligament, however, will admit of a much more interesting interpretation. Its anatomical points must be first briefly considered. It consists of a longitudinal band of dense fibres placed on the anterior aspect (ventral) of the vertebral column, extending from the under surface of the basi-occipital bone with a slight break at the atlas to near the middle of the sacrum; here it becomes scarcely indistinguishable from the periosteum, but as it nears the coccygeal vertebræ it again becomes prominent, and ends at the tip of the coccyx. The superficial fibres extend over several vertebræ (four or five), the intermediate ones pass over two, whilst the deepest fibres only connect adjacent vertebræ.

On widening our view, by extending our observations to other forms of Vertebrata, we quickly become impressed with the fact that this ligament is almost as constant as vertebræ, from the Sturgeon or Perch, Frog or Lizard, Kangaroo or Lion, up to Man. But what is very significant is the large size of the anterior common ligament, especially in Amphibia and Lacertilia, totally out of proportion to the size of the animal, or any function

it may subserve in keeping the parts from any undue separation. This fact would lead one to suspect that it has a morphological significance. The following is my interpretation of the matter:—

The Subnotochordal Rod.—In all Ichthyopsida (Fish and Amphibians), at a period slightly subsequent to the formation of the notochord, there appears a rod-like thickening, split off from the dorsal wall of the alimentary canal. This singular body is known to embryologists as the subnotochordal rod. Its situation and appearance are drawn by Goette, in sections of *Bombinator igneus*. The rod lies between the notochord and alimentary canal, and is of almost the same longitudinal extent as these two structures.

It was first detected by Goette, who gave an account of it in Schultze's *Archiv. für Mik. Anat.*, 1869. In his elaborate account of the *Entwicklungsgeschichte der Unke (Bombinator igneus)*, 1875, he refers to it under the name of *der Axenstrang des Darmblattes*, and suggests that later it becomes a lymphatic trunk (page 775). The subnotochordal rod had been observed independently by Prof. Semper, and Balfour has given a description of it in his account of the development of Elasmobranch fishes.

It is now known to be present in the embryos of Elasmobranchs, Ganoids, the Teleostei, Lamprey, and in the Amphibia, in all of whom it develops in fundamentally the same way.

Although it has not yet been found in a fully developed form in any amniotic vertebrate, nevertheless a structure which in all probability is a rudiment of the subnotochordal rod was detected by Balfour and Marshall as a thickening of the hypoblast in the neck of chicks.

Salensky has further shown that in the Sturgeon (*Accipenser*) the subnotochordal rod becomes in the adult the subvertebral ligament, an observation which, according to Balfour, confirms an earlier suggestion made by Bridge.

This point is important, and it will be interesting to endeavour to extend this view to Vertebrata in general, and show that the *anterior common ligament of the spine results in some forms at least from the degeneration of the subnotochordal rod*, in the same way that ligamentous tissue in various parts of the adult column is the vestige of the embryonic notochord. I have made a series

¹ *Entwicklung der Schildkröten*, page 83.

of observations on tadpoles of the Common Frog (*Rana temporaria*), and have been able to satisfy myself that in this case, after the disappearance of the subnotochordal rod, a band of tissue can be seen in the sections replacing that structure. Further, as chondrification proceeds in the tissue lying between the notochord and the subnotochordal rod, the latter can be seen to become flattened out over the body of the future vertebræ and finally assume a fibrous appearance, and, having degenerated into fibrous tissue, it grows with the vertebral column. Plate III. fig. 16, shows at a glance a stage in the development of the subnotochordal rod and its final transformation into the anterior common or sub-vertebral ligament of the adult Frog. It may be argued that, even admitting this to be true, so far as Amphibians or fish are concerned, yet it cannot apply to vertebrate forms above that group, in whom, with the exception of the chick, a subnotochordal rod has not yet been demonstrated. However, its existence in fish and Amphibia is indisputable, therefore we may assume, unless later on its presence may be detected in higher forms, that the process has suffered abbreviation, and that the anterior ligament appears in these forms in obedience to the great principle—heredity. In support of the notion that this anterior common ligament may represent the subnotochordal rod of Sauropsidia, without actually existing in the peculiar condition it presents in those forms, I would draw attention to the fact that although Comparative Anatomy shows incontestably that the various structures about the knee-joint—ligaments and fibro-cartilages—are in reality the disguised remnants of the tendons of muscles, yet during the development of the human embryo, as Barth has shown in an interesting article ("Die Entwicklungsgeschichte der Menschen," *Morph. Jahrb.*, Bd iv. S. 403, 1878), the various ligamentous elements of the joint arise as thickenings of the connective tissue. In this case, as in so many others, embryological testimony will not always satisfy our demands when we ask for ancestral history, because the process has become abbreviated; hence we are driven to Comparative Anatomy.

I shall now proceed to give a summary of the principal ligaments and ligamentous structures dealt with in this article.

Before doing so, it may be well to remark that, whilst investigating the ligaments with which this article is specially concerned, in no case did I fail to test the accuracy of my previous accounts of the nature of ligaments. I have found nothing that has led me to alter my views on the matter, but, on the contrary, the facts which have come to hand confirm them in every respect.

SUMMARY.

The subjects dealt with in this paper may be briefly summarised as follows:—

1. The semilunar cartilages of the knee-joint are undoubtedly derived from the metamorphosis of muscles, due originally to the change of an animal's habits from a purely aquatic (Urodele Batrachia) to semi-aquatic (Crocodilia) and finally terrestrial life (Mammalia).

2. The bicipital loop in the thigh of birds has had its origin in the metamorphosis of fibres of the gastrocnemius muscle; and that the outer head of this muscle in birds represents the *peroneus primus* (of Mivart's nomenclature) in Lacertilia, but the fascia prolonged from the biceps femoris in most mammals, including Man.

3. The gleno-humeral ligament (ligamentum teres of the shoulder-joint) is present in a very great number of mammals.

4. The "os centrale" of the human carpus is frequently represented by a ligament passing from the scaphoid to the os magnum.

5. The anterior annular ligaments of the ankle-joint of mammals are distinct structures. The superior one arises simply as a thickening of the connective tissue consequent on flexion of the limb, and belongs to the leg.

The lower ligament is the property of the tarsus, and was derived originally from the remains of an old attachment of the extensor longus digitorum muscle to the tarsus.

The oblique bar at the lower end of the tibio-tarsus in birds, and the inferior annular ligament of the mammalian ankle-joint, are homologous. This oblique bar is an adventitious ossification and not an essential element of the tarsus.

6. Rudimentary metatarsals, metacarpals, and phalanges in birds and mammals may be represented wholly or in part by fibrous tissue, and even such a large element of the leg as a fibula may be similarly represented.

7. The posterior common ligament of the spine arises as a thickening of the connective tissue between each conjugate ligament. The anterior common ligament is to be regarded as the degenerate representative in mammals of the subnotochordal rod of Ichthyopsida (Fish and Amphibia).

I feel that my work in unravelling the nature of ligaments is open to one objection, in that it seems to have been done in a

piecemeal fashion. When first the task was commenced I never for one moment anticipated having so much good material, and I am thankful that it has come to hand in such a way as to enable me to pursue the investigation with some approach to thoroughness.

EXPLANATION OF PLATE III.

Fig. 1. The femur of *Iguana tuberculata*, showing the femoro-caudal and the relation of its tendon to the inter-articular cartilage of the knee-joint. *B.*, biceps; *I.P.*, ilio-peroneal; *S.M.*, semimembranosus.

Fig. 2. The relation of the tendon of the femoro-caudal in the Alligator (*Alligator Mississippiensis*).

Fig. 3. The bicipital loop in the thigh of *Rufous tinamou*. *G.*, outermost head of the gastrocnemius; *G.S.N.*, the great sciatic nerve.

Fig. 4. The condition of the loop as seen in the thigh of an Emu, (*Dromæus novæ hollandiæ*).

Fig. 5. The wing of the Secretary Vulture (*Serpentarius reptilivorus*) to show the expansor secundariorum muscle and the tendinous representative of the flexor carpi ulnaris muscle.

Fig. 6. The carpus of man, in section, to show a small ligament passing from the scaphoid bone to the os magnum. It is the remains of an os centrale (modified from Quain).

Fig. 7. The ankle-joint of a Cebine Monkey (*Cebus albifrons*), showing the arrangement of the anterior annular ligaments of the ankle-joint.

Fig. 8. The medio-tarsal articulation of a fowl, showing the anterior annular ligaments. No. 1 is a ligamentous, No. 2 is an osseous, bridge, and transmits the tendon of the ex. longus digitorum muscle.

Fig. 9. The osseous loop of the same bird shown separately.

Fig. 10. Distal end of the tibio-tarsus of a very young Ostrich, showing the fibrous loop of the ex. longus digitorum and the so-called ascending process of the astragalus.

Fig. 11. The hind-limb of Salamander, to show the os intermedium.

Fig. 12. The medio-tarsal joint of an Emu, showing the fibro-cartilage in position.

Fig. 13. The upper surface of the cartilage shown separately. *a.a.a.*, the strap-like processes by which it is attached to the tarsal portion of the tarso-metatarsus.

Fig. 14. An inner view of the medio-tarsal articulation of an Emu, showing a ligament (*L.*) which probably represents an aborted hallux.

Fig. 15. The meniscus, which lies between the contiguous surfaces of the vertebræ in many birds. The aperture *A.* transmits, when present, the suspensory ligament.

Fig. 16. Transverse section of the tadpole of a Frog (*R. temporaria*) in whom the legs are just appearing. *S.*, sp. cord; *M.P.*, the muscle plates; *V.*, vertebra enclosing the notochord; *A.C.L.*, the subnotochordal rod has become transformed into the anterior common ligament of the spine.

VITAL RELATIONS OF MICRO-ORGANISMS TO TISSUE
ELEMENTS.¹ By G. SIMS WOODHEAD, M.D., and A. W.
HARE, M.B., of the *University of Edinburgh*.

DURING the last ten years, and especially during the latter half of that period, our views of the physiology of disease, with its associated histology, seem to have passed through a series of changes almost kaleidoscopic in their rapidity and completeness. The era of cellular pathology, which was inaugurated by the observations of Goodsir in our own country, and of Virchow abroad, at one time seemed to be drawing to a close, in so far at least as one could gather from the writings of many advocates of the more recent theories of the micro-organismal origin of disease. Then some of the followers of Goodsir and Virchow were not prepared to admit the important part played by foreign organised elements in producing the various forms of cellular reaction observed in pathological processes; in this, however, they did not follow their masters, the tendency of whose teaching is always in the direction of a diligent search for all possible factors which influence the balance of cause and effect. As an outcome of this, each party has pushed forward on its own line of progress, the one elaborating the morphology and physiology of micro-organisms into a coherent system; whilst the other has observed and systematised the physiology of the cell in all the stages of its growth, and in various conditions of irritation and stimulation, the partisans of each ignoring to a great extent the results obtained in the rival school. This is the probable explanation of the fact that the actual gain to science generally, and to medicine specially, does not in any sense

¹ An abstract of this paper was read before the Royal Society of Edinburgh, July 6, 1885. The observations on which it is based were made in the bacteriological laboratories of the University of Edinburgh. Such increased facilities for making these observations are now provided in the departments of Practice of Physic, Surgery, and Pathology, that one is led to expect that advanced students and medical men will make use of them, under the guidance of the several professors, in attempting to solve some of the problems to which the germ theory of disease has given rise.

correspond to the amount of labour which has been expended on these studies.

The main facts and principles, as advanced by the leaders in the work, have been confirmed or reaffirmed, and much valuable material, which in the near future may form a basis of further operations, has been accumulated; but as to any development of our knowledge of the relations of micro-organisms to tissue elements in diseased conditions, the outlook at one time seemed far from promising. Recently, however, numerous attempts have been made to graft the results of more perfect methods of observation on the fundamental theory of cellular pathology. The pathologist, as a student of biology, is called upon to explain inherited variability in cells, and to interpret aright the numerous processes which, minute or almost imperceptible in the cell unit, in the aggregate constitute a disease. He must also in some cases explain how this unit may be the subject of very material alterations without giving rise to any serious pathological manifestation. Conversely the student of the normal vital phenomena of the cell must necessarily appreciate the striking analogies which exist between morbid and normal cell processes.

Mr Geddes, in a paper "On a Restatement of the Cell Theory," read before the Royal Society of Edinburgh,¹ restates the views of Goodsir and Virchow, that "all variations are ultimately cellular," and then goes on to say that "pathological changes are simply definable as those variations which happen not to be conducive to success in the struggle for existence," and that "variation and disease in the cell are closely akin." Taking these as a statement of the present position of the cell theory, it will be curious to observe how the life cycle, or parts of it, may be traced in those processes which are initiated by the presence of micro-organisms.

Taking the function of cells, Goodsir affirms that growth and secretion are identical in kind, and that "secretion" in the one case, and "formed material" in the other, are external manifestations of the same vital activity in the cell. It is found that these external manifestations can be varied by modifying the conditions by which the cell is surrounded,

¹ *Proc. Roy. Soc. Edin.*, vol. xli., 1883-84, Dec. 3, 1883.

and these modified manifestations must be regarded as an index of the condition of altered function within the cell. That some such idea as this has gradually become prominent is evidenced by the fact, that in most of the definitions of disease it is actually stated that a diseased process is but a variation of the normal physiological process; although this view is seldom carried so far as to include the essential phases of cell variation.

Sanders, in his lectures, defined disease as "perverted anatomical and physiological functions and parts."

Coats¹ says—"It may be said indeed that the pathological processes are merely the physiological ones altered."

Greenfield—"Anything which impairs the processes of life" = Disease.

$$\text{"Health"} = \left\{ \begin{array}{l} \text{Normal structure} \\ \text{" function} \\ \text{" conditions of existence} \end{array} \right\} + \text{Life.}$$

A deviation from any of these theoretically constitutes a disease, but this is not absolute."

Hamilton—"Health is the average condition of a large number of instances, and is purely an arbitrary standard." Hence he supposes that the transition from health to disease must be imperceptible, and that physiological and pathological processes merge into one another.

Ziegler² says—"By disease we merely imply a phase of life whose manifestations deviate in some way from the normal type"
 "the deviation being conditioned by external influences,"
 "the notion of disease is thus at the outset a physiological notion."

We might sum up the definitions of disease in such a phrase as "vital processes under abnormal external conditions." In the present paper we intend to deal with one group of these external abnormal conditions only—that supplied by the presence of micro-organisms.

The subject must be approached in turn from two points of view—(1) as to the nature and function of the external reagent which acts on the cell,—represented in this case by the micro-organism; and (2) as to the nature of the alterations and reactions set up in the element acted upon,—represented by the tissue changes. In connection with these two aspects, some most interesting generalisations may be made, not only as regards the tissues on which the micro-organisms act, but as to the micro-organisms themselves.

It has been proved experimentally that micro-organisms

¹ *A Manual of Pathology*, p. 2, 1883.

² *General Pathological Anatomy*, Macalister's translation, London, 1883, p. 4.

act upon complex nitrogenous bodies, as do several classes higher in the organic scale, *e.g.*, animals and insectivorous plants, by a process very nearly allied to true digestion. Their function from a chemical point of view, as Frankland has pointed out, is analytical and not synthetical, and by this difference they are at once widely separated from the majority of the more specialised members of the vegetable kingdom.

Their vital action is found to carry out this idea of their classification as Ferments, for they at once fall under the chemist's definition of this class. Hoppe-Seyler¹ defines them as "organic substances, which are themselves easily alterable, are constantly endowed with the power of decomposing H_2O_2 , and with the addition of watery elements are capable of changing organic matters, in such manner as to produce bodies of a less heat-producing power than those from which they have been derived. They produce this effect only within certain limits of temperature; they are destroyed at or before reaching a temperature of $100^{\circ} C.$, most of them in fact, at $60^{\circ} C.$, in the presence of water; and they appear to be in no way disorganised by the fermentative processes to which they give rise." In carrying on their analytical functions the same sequence is followed as in the digestion of albuminoid matters by animal digestive secretions. For instance, from an insoluble albumen, as fibrin, there is first formed a globulin substance akin to myosin. Subsequently peptone, ammonia compounds, leucin tyrosin, indol, and butyric acid may make their appearance. In the long-continued action of such ferments, the peptones formed are themselves broken up, after a certain stage, into simpler products, such as CO_2 and H . The process may be characterised as one of disintegration, in which insoluble complex substances become less complex, soluble, and hence absorbable. Further than this, Pasteur has recently expressed the opinion, based on numerous analogies, that perfect digestion in animals cannot take place without the presence of micro-organisms, and that it is by their aid that the series of analytical processes is carried on by which insoluble albuminoids become soluble and susceptible of absorption, and Duclaux has found that the process of caseation observed in tissues invaded by certain

¹ *Physiologische Chemie*, p. 118, Berlin, 1881.

organisms (tubercle), is due to, or at least advances *pari passu* with, the production of a ferment, which has the same action upon milk as trypsin or pancreatic juice. It is only when the ferments they produce have acted upon the tissues that micro-organisms can obtain food in a soluble and absorbable form which they can apply to their own nutrition and development. They live, as it were, only by actively preparing their own food. The soluble material thus produced is not, however, applied solely to the uses of the micro-organisms. The same soluble products of the ordinary processes of digestion are equally well adapted for absorption by the tissue elements of the animal within which these processes occur. Digestion then, from this point of view, is a process of fermentation, in which the micro-organisms do not utilise the whole of the material on which they act, but set free a very large proportion of elaborated food material, which may be applied to the uses of the organisation in which the process is carried on. In the tissue of their host this same law holds true. The micro-organisms elaborate a ferment, the action of which is to digest surrounding tissues and to render them capable of being applied to the nutritive requirements of the organisms themselves.

It must be remembered here, that in the case of no organism is one product and one product *only* evolved. Taking the yeast plant as a type, we find that alcohol and carbonic acid are not the only results of its activity. It produces also fat, and cellulose, and such quantity of its own complex cell-substance as will provide for its large increase in aggregate bulk. So in the various species of organisms that we have to deal with, the elaborated products, though in the main similar to one another, comprise as a rule in each case a minute quantity of a specific substance, and it is this substance which in pathogenetic species appears not only to render dead material soluble and absorbable, but to prepare living or only slightly devitalised tissues for further assimilative processes on the part of the organisms. But beyond this, in some cases, a product is elaborated, which, acting as an antiseptic, destroys the vitality of the organism which produced it.

The existence of these special products is now generally acknowledged. They are not necessarily accompanied in their

distribution by the organism which produced them, from their greater diffusibility. The organism will, however, usually be found at some point whence absorption of its products might occur. In those cases where it is not found in such a position, and where typical traces of its action may be met with, we have abundant evidence that, owing to the exhaustion of the material necessary for its nutrition, it has ceased to exist, but its progeny have migrated to, and are found in, less altered tissues in the immediate neighbourhood, prepared for their reception by the products of the primary fermentative process, and in this way the infective process is continued and extended from point to point. Continuing the analogy between the infective processes set up by pathogenic organisms, and the processes of digestion and fermentation, it will appear that, as in the latter, when one organism has completed its task another steps in and takes its place (as in the case of mycoderma following torula in malted liquors), so in the tissues, after one micro-organism has produced partial disorganisation another may appear and complete the process of disintegration. How frequently, for instance, does a pyæmic condition supervene on a tubercular process. How often has a patient suffering from tubercular abscess of the kidney or of the lung, succumbed at last, not to this disease, but to pyæmia of a well-marked type, in which a poison far more reaching and deadly than the tubercular product has been rapidly generated and diffused through the system, by the introduction of another organism into dead, though hitherto but slightly irritant tissues.

Turning next to the reactions brought about in the cell elements of the invaded tissues, we shall find that the reactionary changes bear a definite relation to the nature of the irritant and the conditions under which it is applied. Under normal and constant conditions, we might anticipate that the cells constituting one of the higher animals would continue to be reproduced at a fixed rate, to perform their function and die, a regular proportion of young, functionally active, and dying cells being maintained throughout; we know, however, that such a cycle, unless interrupted, goes on for a certain period only, and that there comes a time at which reproduction is not equal to removal, and that consequently organic death takes place, and

the species dies out if the process is not again commenced *ab ovo*.

But there are conditions in which there is interference with the regular cycle. The external conditions or moulding forces may be so altered that the reaction of the tissues to these forces manifests itself in a form which varies somewhat from that observed under normal conditions.

In passing, we may note that the same holds true of micro-organisms;—put them under favourable conditions, and each will pass through a definite cycle, manifesting the different stages by definite signs or appearances, and reacting on tissues in the same manner in each case. Alter the conditions, change the nature of the tissues or of the fluids in which the micro-organisms are placed, and there will be altered reaction on their part.

Amongst the various external causes which may modify the life cycle of a cell, are those usually included under such terms as stimulants, irritants, depressants, &c. In studying the phenomena of inflammation, the surgeon is constantly brought into contact with these modifying conditions. Chiene, in his *Lectures on the Principles and Practice of Surgery*, enumerates, as the exciting causes of inflammation—(1) mechanical injuries; (2) chemical agents; (3) heat and cold; (4) putrefaction; (5) foreign bodies, from without or from within. These, with certain predisposing causes, may be regarded as the external modifying conditions under which the reactions of the tissues are markedly altered, and it is to those included under or akin to putrefaction that we wish to draw attention; that is, to those dependent upon the presence and action of micro-organisms.

The mere presence of micro-organisms in the body may, from an etiological point of view, be a matter of but slight moment. They may, as a matter of fact, be detected in enormous numbers on all the free cutaneous or mucous surfaces, but, in a healthy body, they do not pass further; they are most definitely confined to these positions, and one of the most difficult problems to be solved is met with at the very outset,—what prevents the entrance of these micro-organisms into the tissues, and why do they not migrate from free surfaces to the deeper tissues?

Lister maintains that the chief factor in the prevention of this invasion is the vitality of the tissues, and that this rule

holds good, not only as regards healthy superficial tissues, and those more deeply situated, but that it is also true of two perfectly healthy mucous membranes, or even of two fresh cut surfaces when brought into close apposition. Micro-organisms can neither enter nor develop in healthy tissues, should they come in contact with them. He illustrated these points by a reference to the phenomena observed in the urethra, and in connection with healing by first intention. In a healthy urethra there are no micro-organisms beyond the meatus urinarius, whilst in a wound the presence of such organisms between the two surfaces would be fatal to healing by first intention; a form of healing familiar to all surgeons. Tissues may then be said to have a standard vitality, by the aid of which they can resist the attacks of micro-organisms, but should this vitality be impaired in the slightest degree, an invasion is at once rendered possible. Under normal conditions these minute organisms and their products would be rigorously excluded from the tissues of the body, and it is only when the general vitality of the body is depressed, as by cold, want of food, loss of sleep, and irregular habits, or when there is local depression, as in injuries, catarrhs, &c., that invasion becomes possible.

In the same way, fear, anger, or other strong emotion may act by altering both secreting tissue and secretions, and so interfering with the proper nutrition of the tissues and lowering their vitality. These altered secretions seem to play a most important rôle in accelerating or retarding the development of micro-organisms. Some forms of organisms normally present in inconsiderable numbers, and others which under ordinary conditions are altogether absent, may in these altered circumstances make their appearance in enormous numbers, often to the exclusion of those usually met with. Especially is this the case where, in addition to the alteration in the secretions, there is imperfect removal of the excreta. Such retained excreta may become so modified as to constitute an additional source of irritation, and they may be the focus in which soluble irritants are produced, and from which these are absorbed, and so give rise to local or remote reactions. It may here be not out of place to point out how important are the mechanical and structural peculiarities of an organ or part in determining the

reactions of the tissues and micro-organisms upon one another. Under the first heading may be enumerated constrictions, pouches, cavities, and wounds, internal or external, in any of which there may be accumulations of fluids or excreta. Such accumulations afford a capital nidus and supply abundant pabulum to organisms, which without such a resting-place and food could not lay siege even to weakened tissues with any chance of success. They further, by their direct action upon the tissues, greatly diminish the resisting power not only of the tissues with which they are immediately in contact but also of the organism as a whole. How true this is can best be appreciated by those who have had experience of cholera and similar epidemics, of dysentery, of pouched surgical wounds, pneumonias, and other conditions where irritant accumulations are present. Under the heading of structural peculiarities of a part, in relation to its power of resistance against the attacks of micro-organisms, come the "structure, function, and arrangement of the epithelium covering the surface; the position of the surface and its relations first to the external world, and second to the deeper tissues, especially to the lymphatics; the number, size, and relations of these lymphatics; the tissues in which they occur; the density, vascularity, and vitality of these tissues and the relations of the lymphatics to the small veins."¹

Wood and Formad² pointed out how important several of these factors are in connection with diphtheria, and similar importance may be attached to them in almost all other conditions that are associated with the multiplication and development of micro-organisms in the tissue. In tuberculosis, for instance, which for the present we may regard as "a specific infective disease due to the presence and activity of a certain minute organism, how is it that certain individuals are attacked whilst others escape, that in those attacked the organ most frequently assailed is the lung, and that the selective process goes a step further, and that the apex of the lung is specially affected?"³ In the case of the mouth, fauces, trachea, and air passages generally, it may be easily understood that these are not affected by the

¹ *Pathological Mycology*, p. 5.

² *Nat. Board Health Bull.*, Washington, 1880.

³ *Path. Mycology*, *loc. cit.*

bacillus, as "there is a continual emptying of these cavities, a constant ebb and flow of air, and also of the materials which this air carries with it." Such a state of unrest is fatal to the growth of most micro-organisms. This tidal change is found in the whole of the healthy lung in which there is full expansion and contraction. As has been fully recognised by the older physicians, such expansion and contraction fail first at the apex, the tidal change ceases, and phthisis, *post hoc*, and, as this would indicate, *propter hoc*, first manifests itself in this position. In the lungs of children where there has been great enlargement of a bronchial gland, or where from any other cause there has been pressure upon and partial or complete closure of a bronchus leading to one of the lower parts of the lung, the tubercular nodules appear first not at the apex necessarily, but in the lower area in which the tidal change is incomplete or absent, and where in consequence there is an accumulation not only of what enters or has entered, but of what normally should escape.

A bacillus effecting an entrance to an air vesicle in either of such areas has everything in its favour. "It is not readily dislodged, it is at rest, it is supplied with ample food stuff, it has an altered epithelial surface on which to act, and it is on a surface between which and the neighbouring lymphatics there is the closest communication." In the upper part of the respiratory tract all the structural peculiarities are against the bacillus. In the mouth there is a thick covering of squamous epithelium, which can withstand the attacks of the most vigorous micro-organism (unless it develops with extreme rapidity), and so act as an impassable barrier between the micro-organism—in this case the tubercle bacillus—and the lymphatics. In the lower parts of the respiratory tubes there is still an epithelial barrier in the form of well-developed ciliated columnar cells. It is the function of these cells to pass on from one to another along with mucus, particles of dust, &c., the bacillus which is seeking lodgment for a sufficient length of time to be able to develop morphologically and physiologically. That invasion of these tissues but seldom occurs is evidenced by the extreme rarity of tubercle in the positions above mentioned except towards the termination of a case of tuberculosis. In the terminal air cavities, however, as we have already seen, there is almost

perfect rest under certain conditions, the tissues are less resistant, there is no continuous transference of secretion which might help in the removal of the bacillus, the lymphatics are readily reached, and the bacilli, with everything in their favour, carry on an attack which results in tuberculosis.

Apart from such obvious structural characteristics as those above mentioned as favourable to their ingress, the question as to the invasion of the deeper tissues by micro-organisms is one that presents many difficulties. The means by which the micro-organism retains its vitality until it reaches a weak point must for the present remain a matter of conjecture. It might be supposed that the transference through the healthy tissues is so rapid that the organism does not lose its vitality nor its power of attacking the devitalised tissue. Or, it might be suggested, that it is protected by the material in which it originally flourished, a part of which is carried along with it, or by surrounding organisms which, although themselves devitalised, form a protecting shield around it.

A general classification of the action of micro-organisms, based on the clinical characters and localisation of the invasions, may be drawn up: and working on this classification these different modes of action directly upon the tissues, or on the organism as a whole in different diseases, may be stated as follows:—

1. As in the soft sore virus this action may be purely local and confined to one area, beyond which neither the micro-organism nor its products have any effect.
2. There may be a purely local action in the first instance, but this localisation is only temporary. The invasion goes on in stages, point after point being attacked. The spores developed at one point are transported to others, and so the process goes on intermittently, as in actinomycosis.
3. The organism may be limited to a definite tract, but its products may be diffused throughout the whole of the invaded organisation as in certain cases of septicæmia.
4. There is no limitation to the sphere of activity of the micro-organism, which with its irritant products may penetrate to all parts of the tissues, and so give rise to a general disease, as in the case of the organisms which give rise to the specific fevers.

In all these cases several factors must be taken into account in considering the changes which result from the presence during their life-history of micro-organisms in the tissues.

(A.) They may act merely as mechanical irritants, just as so many particles of carbon or of stone when taken into the lymphatics of the lung. In stone masons' phthisis, for instance, the granulomata met with are, during certain stages, almost identical in appearance and in structure with those found in a case of chronic tuberculosis. Further, the changes in the adventitia of the vessels of the lung and the *arteritis obliterans* observed in these vessels are optically identical in the two diseases; and the gummatous masses met with in stone masons' lungs are formed in much the same manner as are tubercular caseous masses and caseous syphilitic gummata. These are at least to some extent due, as maintained by Heubner, Friedlaender, Greenfield, and others, to a cutting off of the blood supply through the complete obliteration of the arteries which originally supplied the caseating area. Thus, the mechanical action of unorganised foreign elements demonstrates at least the possibility that organised foreign elements act in a similar purely mechanical fashion.

(B.) That this mechanical action does not explain all the phenomena observed in bacterial invasions is proved by the fact that marked tissue changes are found in regions remote from those in which the pathogenetic organism occurs. Even in the locality where bacteria are present, certain tissue reactions are observed, which cannot be explained except by the theory that there is present an elaborate chemical irritant; an instance of this is supplied by the necrotic changes observed by Pasteur in the muscle of a fowl at the seat of inoculation in chicken cholera. It would appear then that the micro-organism during its life cycle produces an irritant product or ptomaine, which, in some forms, is so constituted that it can act merely locally, whilst in others it is capable of rapid absorption and transmission by the tissues, and produces, in consequence, general and far-reaching effects on the organism.

(C.) In the third place, it is probable that in certain forms there is, in addition to the above factors, a more subtle physico-chemical or molecular reaction between the micro-organisms

and the tissue elements which may give rise to local or general changes, such changes being comparable to those brought about by the action of the sperm cell on the germ cell or ovum. In addition to the foregoing general features of bacterial action, the five following types of tissue reaction may be taken as illustrative of the principal pathological processes of micro-organismal origin.

1. *Septicæmia*.—in which there is an absorption of septic products from an external or localised internal source, but no absorption of the organisms which give rise to them. Diffusion of products.

2. *Specific Infective Fevers*.—No localised source after period of incubation. General diffusion of both organisms and products.

3. *Abscess Formation*.—Micro-organisms in area strictly localised by "pyogenic membrane." Rapid death of that area.

4. *Tubercle*.—Micro-organisms localised. Slower death and caseation of area in which they occur. Slight tendency to fibrous tissue formation.

5. *Actinomycosis*.—Localisation of micro-organisms. Comparatively little tendency to death of proliferated cells. Great tendency to fibrous tissue formation.

These types are exhibited in the following tabular form:—

Type.	Distribution of Micro-organism.	Tissue reaction.	Effect.
Septicæmia.	External to tissues, or localised internally.	General (if any).	Rapid toxic paralysis.
Specific infective fevers.	General.	General.	Toxæmia.
Abscess.	Local.	Rapid local death.	Necrosis.
Tubercle.	Local (?).	Degeneration, slight tendency to fibrous tissue formation.	Caseation.
Actinomycosis.	Local.	Greater tendency to fibrous tissue formation.	Fibrosis.

The following points should be noted in connection with the above types of bacterial activity in relation to the tissues.

1. *Septicæmia*.—In the case of an extensive surface injury,

with complete destruction of the epidermis, there is immediate and extreme danger of acute septicæmia from the use of dirty dressings, or from other causes of infection, such as are met with in large hospital wards. The devitalised tissues, bathed with abundant moisture, and kept at the temperature of the body, constitute an excellent culture surface on which septic organisms flourish most luxuriantly. These, without passing into the deeper tissues, develop an absorbable ptomaine in sufficient quantities to kill the patient.

In proof of this, it has been found that alkaloids formed during the decomposition of animal matter, when carefully separated and introduced into a vein or even into the connective tissue, produce rapid death by general toxic paralysis. Should there be no immediate absorption, a barrier is formed by the rapid contraction of the cut ends of the blood-vessels, which is associated with a rise of blood pressure and dilatation of the blood-vessels behind the point of obstruction, and consequent exudation. This exudation consists essentially of blood plasma and leucocytes, both of which play an important part in the formation of the barrier which is to prevent the entrance alike of micro-organisms and their products. There is at a very early period a pouring out of the elements of fibrine into the lymph spaces which thus early become occluded at certain points, especially near the injured tissues. Along with this, there is marked exudation of leucocytes from the small vessels, especially from the small veins, and probably also from the capillaries, in both of which there is increased pressure, due to an increased flow of blood, and to obstruction at the cut ends of the capillaries. In consequence of this increased blood supply there is increased nutrition and rapid proliferation of the connective tissue corpuscles.

Here then the capillaries are no longer patent beyond the margin of the dead tissue, the lymphatics are blocked up, and there is a great increase in the number of connective tissue corpuscles or amœboid cells in the immediate vicinity, and there is thus formed a complete vital separation or line of demarcation between the devitalised tissues and those in which repair is to be attempted.

Here there are two sets of tissues, those in which the vitality

is greatly impaired by mechanical or other injury, and which with their impaired vitality can no longer withstand the attacks of various septic organisms. If left unprotected, these dead tissues undergo decomposition, or are digested by the micro-organisms, and in this process of digestion there is an enormous development of ptomaines, so that there are present in this mass of decomposing tissue both micro-organisms and their products.

The second set of tissues consists of those in which the vitality, though slightly, is only partially impaired. In them the lymph spaces, however minute, are filled with active amœboid cells, the source and mode of origin of which for the present may be left out of account, though it is evident that the increase in the number of amœboid cells is connected directly or indirectly with changes in the blood-vessels and lymphatics in and around which they occur.

These amœboid cells appear to act the part of protective elements to the deeper tissues, as they come to the free surface they attack, and, as is now recognised, absorb and digest not only the dead tissues but also the micro-organisms and their products. Metschnikoff¹ contends, in connection with the above, that there is an intimate relation between the presence of micro-organisms and the emigration of amœboid cells. During the process of absorption, although there may be an actual increase in the nutrition available for the use of the cell, the relative nutrition for the increased amount of work the cell has to perform may be diminished, its vitality is impaired, or it may even die altogether. As such cells die, they are thrown off from the free surface, or some of them are attacked in turn by the active cells behind them, and so the process goes on. The whole process may be demonstrated under the microscope. At a certain stage, however, in consequence of this digestion of the area of dead tissue near the healthy zone, there is gradually formed a mechanical line of demarcation, and the slough or mass of dead tissue separates. With it is removed one of the great dangers to the patient, for the large ptomaine factory is removed and a clean granulating surface is left. Such a granulating surface is always considered by surgeons to be non-absorbent, and so it appears to be so far as micro-organisms

¹ "History of Inflammatory Process," *Quart. Jour. Micr. Sci.*, January 1884.

and their products are concerned, though this may be only partially true, as certain other vegetable alkaloids appear to be readily absorbed from such surfaces. This non-absorption is, however, more readily understood, if one bears in mind that the amoeboid or digesting cells near the surface become inert as their vitality is lowered, or that, as their protoplasm is overstimulated, disintegration follows, the dead corpuscles are thrown off on to the free surface, and fresh cells from behind take their place. The only conditions now under which micro-organisms have any chance of invading the deeper tissues, is through fresh injury of the granulating surface, on which there is a great accumulation of dead or partially devitalised cells, which serve as pabulum for the ptomaine producing bacteria. The ptomaines produced in this position are ever ready to enter at the smallest breach.

The importance in surgery of (1) getting rid of all sloughs as early as possible; and (2) of making provision, by means of frequent dressing (in septic wounds), for the continuous removal of the separated or pus cells, and with them the micro-organisms and their ptomaines, is now generally recognised.

2. In the case of the *specific fevers* there is, as in septicæmia, a general distribution of toxic material through the system; but here, not only are the irritative products widespread, but also the micro-organisms which produce them. The organism is thus involved in a general invasion, which puts to the test its powers of resistance as a whole. In this type of morbid action a "crisis" frequently occurs, depending upon a summation of resisting efforts on the part of the tissues, or on the exhaustion of the irritative activity of the attacking organism; in either case the poison and the organised ferment which produces it are thrown off by the excreting tissues of the invaded organism. The special channels through which this elimination is effected in the different fevers have not yet been clearly defined; but it has been proved that the kidney has an important function in this respect in many of these diseases, as has also the skin in the case at least of those of an exanthematous type. The evidence collected on these points is as yet very slight, and does not countenance the adoption of more definite views on the subject.

3. In *abscess formation* both the elaborated irritant and the micro-organism which produces it are strictly localised in their distribution in the tissues.

"In the case of an acute abscess, an indurated mass of tissue is first noticed. If this be punctured, no pus escapes; the tissue reaction has not yet reached the stage of pus formation, but a drop of perfectly clear serum exudes from the centre of the mass. On examination this is found to consist of a few lymph cells and immense hosts of chain or cluster-forming micrococci floating in the lymph. If this puncture be repeated in twenty-four hours pus is found to be present in small quantities, loaded with the same organisms. If repeated punctures be made at intervals, an increased quantity of pus is found each time, and the organisms from the commencement of pus formation begin to decrease, till, in an old abscess of some weeks' standing, no living micro-organisms are present; but the pus is found to contain dead micrococci, not readily recognisable, as they are partially broken down and take on staining reactions very feebly. The reason of this sequence of phenomena is, that after attaining their maximum degree of development in a locally devitalised portion of tissue, the micrococci are prevented from further progress by the zone of fully vitalised tissue around; and the powerful vital reaction in this zone hems in the organisms on every side, and at the same time limits the formation of pus to the centre of the affected locality. The micrococci soon exhaust all the supplies of pabulum at their command, and then rapidly die out, being in many cases destroyed by their own effete products in the pus; and in pus taken from long unopened abscesses they have quite disappeared. Thus the presence of micrococci in the tissues precedes the reactionary changes to which they give rise locally in the case of acute abscesses."¹

These reactionary changes result in the rapid necrosis of the portion of tissue attacked, beyond which, however, any invasion, whether of the ferments or of their products, is prevented by the strongly reacting zone which surrounds them.

4. In *tuberculosis* both the organised ferment, and its irritative product are localised in their distribution; but their effects are not so closely circumscribed as in the case of acute abscess formation. The distribution of tubercle bacilli in the affected areas of the lung throws some interesting light upon this question.

"Taking the centre of a lobule, usually the bronchus, as the point from which to commence the observation, it will be noted that in this bronchus, and in the air vesicles immediately surrounding it, caseation has become a well-marked process. In the caseous mass bacilli are found (in the specimens under consideration) in enormous

¹ *Pathological Mycology*, p. 7.

numbers. Passing from the caseous centre, it will be found that where traces of the original structure exist, the bacilli are still present, but are not so numerous as in the centre. Extending the observation to the margin of the tubercular mass, it will be noticed that there is an area of active cell proliferation, not confined to the endothelium of the lymphatics, but appearing also in the epithelium of the air vesicles. In this mass of proliferating tissue there are absolutely no bacilli at first; a few may be distinguished, here and there, near the proliferating area, but where the proliferation is most marked, the bacilli are absent. In a very large number of sections examined this was invariably the case. This can be best accounted for on the theory that the bacilli during their growth and development secrete or excrete a chemical substance which alters the activity or vitality of the cell from its original resistant and stable condition to one in which there is an increased vegetative activity, but a diminished resistant power to the action of the bacillus itself. The highly organised proteid of the cell is thus rendered available as food for these minute organisms, which advance in the track of their chemical vanguard, and continue the process of disorganisation and disintegration.

"In old tubercle masses the result of this process appears in the form of caseous debris, from which all tubercle bacilli may have disappeared, as they have selected what they required, and have exhausted the materials which were necessary for their maintenance; but whilst doing this they have, by setting free their diffusible ferment, prepared the tissues in the immediate neighbourhood for the reception of their progeny. In this way the process is continued and extended."

In acute tuberculosis, as above described, the degenerative changes ending in caseation and complete disintegration of the tissues, constitute a destructive type of activity. In certain forms of tuberculosis, however, where it runs a more chronic course, this is modified, and its place is taken by a formative activity on the part of surrounding tissues, ending in fibrous tissue formation. This occasional outcome of the tubercular process links it closely with that next to be described (*actinomycosis*) where such an outcome is of very frequent occurrence.

5. As an example of the fifth type may be instanced one of the granulomata, in which the relation between the fungus and the granulation tissue is very distinctly marked, and in which the action of the fungus is at first extremely well defined, though it afterwards may give rise to secondary growths at a distance. In *actinomycosis*, a condition induced by the presence in the tissues of the "Ray fungus," many important features of parasitic invasion are strongly accentuated, and in it one may study the

method of invasion and the subsequent course of events perhaps more readily than in any other growth of bacterial origin.

It is very generally acknowledged that the fungus may be present in the glands of the mouth and tonsils, as has frequently been pointed out in the case of the tonsillar glands of the pig. Here, so long as there is no abrasion and no inflammatory process, the fungus and its spores are perfectly innocuous. If, however, the epithelium of the glands be detached, or if even a few cells be removed, the spores are carried into the lymphatics, and in time a regular actinomycoma results.

From a careful examination of a number of specimens from four cases of this affection (wooden tongue of the cow in each case), we have come to the conclusion that the presence of spores alone does not set up any very active cell proliferation. In many of the specimens stained with picro-carminc numerous spores may be found, as small bright yellow rounded bodies, grouped together or single, lying in the lymphatic spaces, especially in those around the blood-vessels. Although there is evidently no cell proliferation around the single spores, it seems as though there is a slight increase in the number of small round cells around the clusters.

Where, however, there is development, incomplete though it be, of the actual Ray fungus, there the development of new cells becomes a marked feature.

These facts point to the secretion of an irritant material, which acts not only in the immediate neighbourhood of the fungus, but also within a well-defined radius around it. How otherwise is it possible to account for the commencement of cell proliferation in the immediate neighbourhood of the fungus only, or where a number of spores are grouped together, and where there would be probably carried with them a considerable quantity of the secretion.

If one of the small circumscribed nodules be examined it will be found that occupying the centre is the Ray fungus, around which, and apparently in close contact with the gonidia, are numerous epithelioid cells. Some of these cells have a single nucleus only, whilst others have several surrounded by a definite protoplasmic mass. In some specimens there is in addition a network of formed material on which the cells rest.

It is rather a curious fact that in direct contact with the fungus we have these epithelioid or endothelioid cells, and that it is not until the margin of the nodule is approached that small round or granulation cells are to be met with. Along with these granulation tissue cells, which are almost invariably accumulated in distended lymph spaces, are numerous flattened or spindle-shaped connective tissue corpuscles, branches of which clasp bundles of fibrillar tissue.

Outside the granulation tissue area a zone of dense fibrous tissue is frequently observed, forming a line of demarcation between the nodule and the surrounding tissues; but even in this, some of the lymph spaces are distended with small round cells very similar in character to those already described as present in the lymph spaces beneath a granulating surface.

In such a case as the above, it can scarcely for a moment be doubted that the granulomatous masses are most intimately connected with the invasion of the tissues by the Ray fungus. Typical nodules are found only where the fungus is in active growth; the fungus is never found without the granuloma, and in these cases the granuloma is never found without the Ray fungus, and they must, so far as at present appears, be looked upon in the light of cause and effect. The mechanical presence of the fungus may give rise to the proliferation of cells in its immediate vicinity; but how, without the aid of some chemical agent formed by the fungus itself, or as the resultant of the action of the fungus on the tissues, can we account for the enormous increase in number of the amoeboid cells in the lymph spaces. These amoeboid cells seem to have several functions, the chief of which, however, is digestive, for by their presence they form a barrier beyond which the ptomäine or active stimulating reagent is comparatively powerless. Not only do these cells absorb the ptomäines, however, but they absorb also the formed or fibrillar material in their immediate neighbourhood, and thus get rid of the comparatively non-resistant material, and so remove or apply to their own uses material which would otherwise form food-material for the growing fungus, thus limiting its power of growth and reproduction. This absorption of formed material may be observed in all cases of inflammation, and has a most important bearing on the process. As a result of this zone of

demarcation it is found that immediately outside, the proliferative activity of the cells is diminished as they are less stimulated, and such cells settle down into the encysted stage; a large quantity of formed material is accumulated and a fibrous zone or capsule is produced around the granulation mass. From the constant presence of this zone of fibrous tissue it may be said that a constructive type of inflammation predominates in actinomycosis.

One of the most interesting points brought out by a study of the granulomata, such as those above described and those met with in syphilis, is that the giant cells, properly so called, as well as the large endothelioid cells, are connected with organisation and not with degeneration. They are to be looked upon as cells in which the constructive activity predominates, and their presence indicates that the efforts put forth by the tissues to get rid of bacterial irritants are not entirely without success. If one examines an abscess in which bacteria are present these endothelioid cells are found only in the zone of resistant tissue and usually outside the zone of amoeboid cells. These endothelioid or "fibro-plastic" cells are here present in large numbers, and have evidently an intimate connection with the localisation of the micro-organisms, if not as cause, at least as effect. In chronic tuberculosis this relation of large multinucleated endothelioid cells is very well seen, whilst the converse holds good in acute tuberculosis, where, except at the very commencement of the process, these cells are relatively far from numerous. Similar observations may be made in syphilitic granulomata, in glanders nodules, and allied growths. Without attempting to enter further into the description of the processes involved in tissue reaction in each of the classes above named, we may briefly summarise the main features, and illustrate them by one or two examples. Amongst the chief forms in which cell activity exhibits itself during various stages of the biological cycle, are, according to Mr Geddes—(1) The amoeboid stage, where nutritive activity is well marked, but where formative activity is not yet distinctly manifested, as the nutritive requirements of the cell are in excess of, or are at least equal to the amount of material presented to it or taken up by it. Here the irritation to which the cell is exposed is a most important factor, the activity of the cell is enormously increased in many cases, and

the amount of nutrition required is proportionately increased; unless this increased quantity is supplied there is always the tendency to proliferation of the cells rather than to a condition in which the formative power of the cell can be manifested.

(2) Then, where there are both excessive stimulation and excessive nutrition, we have the plasmodial stage, in which, owing either to aggregation of cells or to imperfect division in a cell there are formed large multinucleated masses of protoplasm, in which the vital activity of the component individual cells is not only summed but multiplied in the resulting plasmodium. In this form of cell there is a latent formative tendency, which comes into play on the removal of the excessive stimulation. These cells might be compared with the parablast of an embryo from which the excess of nutritive material is handed on to other cells in the blastoderm proper. In this parablast we have a large mass of protoplasm embedded in which are numerous free nuclei. It appears to act the part of a yolk digester for the supply of food to the growing blastoderm.

(3) In the third or encysted state the formative activity is a more prominent feature than the nutritive function, and the cell gradually assumes a condition of quiescence, as in the formation of fibrous tissue.

In normal tissues under normal conditions the metabolic processes balance one another. If, however, the tissues be irritated, this balance is lost. There is increased activity of the cell, during which the process of "aggregation" is well marked; as, for instance, in cloudy swelling of the cells of various organs during the early stages of specific infective fevers. Here, although the amount of food material actually assimilated may be increased, the amount relatively to the increased activity of the cell may be diminished, with the results above stated.

If the irritation is continued, the above stage may be followed by an increased digestive power or nutritive activity, such as is found in the plasmodial stage of the cell cycle. Here again, however, should the irritant be excessive, complete "aggregation" or "cloudy swelling" followed by disintegration takes place. Should the irritation be not excessive, formative activity manifests itself, and we have as a result a tissue formation and a stage corresponding to the encysted cell. All the above stages.

may be traced in one or other of the examples of micro-organismal irritation noted under the headings of Abscess, Tubercle, Antinomycosis, &c.

From Marshall Ward's recent researches on the mode of reproduction in certain cellular organisms,¹ it appears that it is possible for a parasitic fungus to reproduce its like without the direct aid of a sexual process, the necessary stimulus to multiplication being supplied by the highly organised proteids derived from the tissues of its host, which, in their turn, are also stimulated into proliferation. Applying this to the case of cells in an animal, it would appear that the stimulus applied by the presence of micro-organisms or their chemical products acts in a manner comparable to the action of the male element upon the ovum in setting up segmentation. There is thus a reappearance of excessive reproductive activity without a re-initiation of the process *ab ovo*. As pointed out by Charles and Francis Darwin, in connection with their researches on insectivorous plants, cell proliferation can be set up by effete products or other chemical irritants, or even by mechanical irritants, and the reactions thus variously produced, though differing greatly in degree, are absolutely one in kind. Apply any irritant to a surface or a tissue, and there results a cell proliferation, especially in the connective tissue group, where the increase in the number of cells is extremely marked. With this increased cell formation there is apparently a taking up of the irritant material by the cells, and if one cell is not sufficient for the task, a number combine to form plasmodia or giant cells. That the taking up of these products or the micro-organisms themselves further lowers the vitality of the cell may be inferred from the fact that, as soon as it becomes filled with the irritant particles, it dies, and with its contained material acts as an irritant to other cells. The chemical products then may be looked upon as the prime movers in bringing about a proliferation of the cells with which they come in contact, which proliferation is an indication of an effort on the part of the cells to get rid of the irritant material by which their resisting power is subjected to so great a strain.

¹ H. Marshall Ward "On the Sexuality of the Fungi," *Quart. Jour. Micros. Sci.*, April 1884.

In the foregoing brief sketch we have attempted to give a summary of the pathological processes in which micro-organisms are present as causal agents; and we have endeavoured to bring forward evidence in support of the theory propounded by Goodsir and Virchow, that pathological processes, as observed in cells, are simply physiological processes under abnormal conditions.

THE BLOOD-FORMING ORGANS AND BLOOD-FORMATION: AN EXPERIMENTAL RESEARCH.¹ By JOHN LOCKHART GIBSON, M.D., *formerly Senior Demonstrator of Physiology, University of Edinburgh.*

IN publishing a Thesis which, as may be inferred from its title, had necessarily to be a long one, and therefore could not all appear in one number of a journal, I find it advantageous to divide it more distinctly into three parts than I did when sending it in manuscript form to the University.

As it is necessary first to come to as clear a conclusion as possible with regard to the number and nature of the elements found in the blood, before proceeding to inquire into the organs which produce them, the first part of my paper will be on the elements "found" in the blood in addition to the red and white corpuscles. The second part will deal with the blood-forming organs, including the spleen, bone-marrow, and lymphatic glands. The third part will deal with the thyroid gland.

PART I.—ON THE ELEMENTS "FOUND" IN THE BLOOD IN ADDITION TO THE RED AND WHITE CORPUSCLES.

The elements "found" in the blood in addition to the ordinary red and white blood-corpuscles, are four in number; although some would consider that the number three would include them all. Concerning these additional elements, there is much confusion and much difference of opinion; as will readily be understood, when I mention that each of the several "discoverers" of three of them considers his element to be the forerunner of the non-nucleated red corpuscle found in the blood.

In this portion of my paper it will be seen that, partly from my own observations and partly from those of Neumann and Bizzozero, I have been able to form pretty definite opinions with regard to these elements; so that my readers, before proceeding to the blood-forming organs, will have a knowledge of what elements have in my opinion an important relation

¹ This Research was presented to the Medical Faculty of the University of Edinburgh, in April 1885, as a Thesis for graduation as Doctor of Medicine; and a Gold Medal was awarded for it on August 1.

to blood-formation, as well as of what elements it will, according to the view I take, be unnecessary for us to consider further.

First, we have those elements which have often been called the "corpuscles of Neumann," but are more correctly called "nucleated coloured corpuscles." These are cells which, in their most typical form, are identical with the nucleated red corpuscles found in the blood of the fœtus. They were found by Kölliker¹ in the liver during the whole of intra-uterine, and at the beginning of extra-uterine, life; and were supposed by him to be formed there, and to be the forerunners of the non-nucleated red corpuscles. They were again prominently brought forward by E. Neumann² in 1868, and shortly afterwards by Bizzozero,³ as being found in the red bone-marrow throughout the whole of life. They are occasionally found in the circulating blood (Neumann and others), when the blood-forming process is active. In their most typical form, these nucleated red corpuscles are slightly larger than a non-nucleated red corpuscle, and have a nucleus which is colourless, and which is not relatively large as compared with the size of the cell. They will be considered more particularly in the second part of my paper, where I speak of blood-formation.

The *second* and *third* varieties of elements found in the blood, at any rate after it is drawn from the vessels, must be considered together; for, although they appear to me to be two distinct elements, they have been much confused, and are generally described as one and the same element.

These elements have lately been rediscovered by Hayem⁴ and Pouchet,⁵ under the name of "hæmatoblasts" (Hayem) or "globules of Donné" (Pouchet). As described by Hayem and Pouchet, they are oval in shape, except in the case of the very smallest; are slightly refractile; are devoid of nuclei; are left unstained by staining agents; approach in their physico-chemical characters the substance of the bodies of the white corpuscles; and exhibit a marked tendency to run together,

¹ Kölliker, *Mikrosk. Anat.*, Bd. ii. p. 590.

² Neumann, *Centralblatt f. d. med. Wiss.*, 1868, p. 689.

³ Bizzozero, *ibid.*, 1868, p. 885.

⁴ Hayem, *Arch. de Physiol. norm. et path.*, 1878, p. 692; 1879, pp. 201 and 577.

⁵ Pouchet, *Quart. Jour. of Micros. Science*, 1880, No 79.

either with one another, with the white corpuscles, or with the red corpuscles, even in circulating blood in normal conditions.

The same elements were discovered long ago by Max Schultze,¹ and were called by him "Körnchenbildungen." G. Zimmermann² also described them, and called them "Elementarkörperchen." Hayem and Pouchet consider, as did also Zimmermann, that these elements are the forerunners of the red corpuscles, and that the red corpuscles are therefore not of a cellular nature.

Hayem and Pouchet differ as to their immediate origin: Hayem saying they arise from the lymph-corpuscles while these are yet in lymph-vessels, while Pouchet, who at first held a similar view,³ believes they arise in the blood-plasma itself, as the result of changes analogous to the precipitation of fibrin. Both of them, however, consider that they have found transition-stages between these "Körnchenbildungen" (to use the name given them by Max Schultze) and the red corpuscles.

E. Neumann,⁴ in an exhaustive and able paper, criticises the views of Hayem and Pouchet, and says that their so-called "hæmatoblasts," and the transition forms between them and the red corpuscles, are the results of retrogressive changes in the red corpuscles, instead of being early stages in their development. He says that in fresh preparations of blood he can see the blood corpuscles losing their colour and shrinking, to leave only a shrunken colourless stroma behind. "This breaking down of the coloured corpuscles, often with the result of leaving behind them discoid, bi-concave, light-coloured corpuscles, is," according to him, "more apt to take place at low temperatures;" and the observations of Hayem and Pouchet were especially conducted under low temperatures.

The view enunciated by Max Schultze, in his criticism of Zimmermann's doctrine, coincides exactly with Neumann's, viz., that the elements in question "are much more likely to be the result of the breaking down of coloured corpuscles than elements

¹ Schultze, *Archiv f. mikrosk. Anatomie*, Bd. i. p. 36.

² Zimmermann, *Rust's Magazin*, 1846, Bd. lxvi.; *Virchow's Archiv*, Bd. xviii. p. 221; *Zeitschrift f. wiss. Zoologie*, Bd. xi. p. 259.

³ Pouchet, *Gaz. méd. de Paris*, 1878, No. 11.

⁴ Neumann, "Ueber Blutregeneration und Blutbildung," *Zeitschr. f. klin. Medicin*, Bd. iii. p. 411.

capable of developing into coloured corpuscles." Riess¹ also calls these elements "Zerfallskörperchen;" and Ehrlich² holds the same opinion.

Neumann very properly objects to Hayem and Pouchet using as a foundation for their hypothesis that these elements are young red blood-corpuscles, the fact that they found a great number of them, and of transition-forms between them and red corpuscles, in the blood of pernicious-anæmia patients. As Neumann says,—“Where, if not in pernicious anæmia, will breaking-down coloured blood-corpuscles be found?”

To the fact observed by Hayem and Pouchet, and confirmed by Riess, that these “Körnchenbildungen” occur in numbers in the blood of animals in which artificial anæmia has been produced, Neumann answers, that the argument put forward by Ehrlich, in his paper above referred to, is the correct one, viz., that the chemical change and thinning of the blood exercises a deleterious influence on the red corpuscles, and causes them to degenerate, and to present the appearance of “Körnchenbildungen.” And Riess and Leube³ criticise the statements of Hayem and Pouchet in the same spirit.

Neumann and Ehrlich both consider that the “Körnchenbildungen” have no connection with the white corpuscles, i.e., are not derived from them.

But before discussing the “Körnchenbildungen” further, I must first mention elements described by Bizzozero,⁴ and considered by him to be identical with those described by Hayem and Pouchet. These elements Bizzozero has called “Blutplättchen,” and has described as follows:—“Very pale, colourless, oval or round, disc-shaped or lenticular Plättchen, from one-third to half the size of the red blood-corpuscles.” He found them in the circulating blood of the mesentery of chloralised rabbits and guinea-pigs, and says that they are scattered irregularly among the red corpuscles. He explains that

¹ Riess, *Reichert & Du Bois-Reymond's Archiv*, 1872, p. 287; *Berliner klin. Wochenschrift*, 1879, No. 47.

² Ehrlich, *Berlin. klin. Wochenschrift*, 1880, No. 28; 1881, No. 3.

³ Leube, *Berlin. klin. Wochenschrift*, 1879, No. 44.

⁴ Bizzozero, “Ueber einen neuen Formbestandteil des Säugetierblutes und die Bedeutung desselben für die Thrombosis und Blutgerinnung überhaupt,” *Centralblatt f. d. med. Wiss.*, 1882, pp. 17, 161, 353, 563.

they have not been found by others in the circulating blood because they are so colourless and transparent, being not only much less numerous than the red corpuscles, but also much less visible than the white; and also because it is so difficult to watch the blood circulating in the mesentery of warm-blooded animals. And he further says that these "Plättchen" are also to be seen in freshly-drawn blood, appear in great part grouped around the colourless corpuscles, and rise to the top of the layer of fluid under the cover-glass." According to him, it is these "Plättchen" that, by their rapid change and running-together to produce granular masses after the blood is drawn, have given rise to the appearance described as "Körnchenhaufen," by so many histologists. He, however, says that, for the purpose of further examination, they can, by means of suitable reagents, be retained in their normal form. He cannot say positively where these "Plättchen" come from, but sees nothing to support the theory of their origin from the falling-to-pieces of the white blood-corpuscles; because, he says, "these Plättchen have a typical form, and the white corpuscles contain nothing like them." He recognises in them the same elements as those described by Hayem, but says that Hayem is in error in describing them as bi-concave discs; and he further considers that they are composed of a substance entirely different from that of the red corpuscles, and that they never contain hæmoglobin. He, like Hayem and others, has observed that they increase in number after hæmorrhage, and in various diseases; and he also considers that the "white thrombi" of the Mammalia are composed of them, and that they probably play the same part with regard to coagulation as Mantegazza and A. Schmidt ascribe to the white corpuscles.

Schultze, Ranvier, Hayem, and others have remarked that the fibres of fibrin radiate from the "Körnchenhaufen"; and have therefore said that there is a connection between these and the precipitation of fibrin. A. Schmidt goes still further, and says that the coagulation of the blood is induced by the white corpuscles, which by their falling-to-pieces produce the "Körnchenbildungen" and resulting "Körnchenhaufen," and that the "Körnchenbildungen" go to form a considerable part of the material of which fibrin is composed.

Bizzozero agrees with these authors in so far as he considers

that his "Plättchen" induce coagulation; but he does not think that they are derived from the white corpuscles, and accordingly denies that these have the power of inducing coagulation. He bases his conclusions that the "Plättchen" are not derived from the white corpuscles, and that it is they, and not the white corpuscles, which induce coagulation on the following:—

1. He has been unable to see the great falling-to-pieces of the white corpuscles described by Schmidt;¹ and accounts for the stated fact that there are more white corpuscles in the circulating blood than in the blood after it is drawn, by saying that the white corpuscles do not easily pass out of the wound in the vessel.

2. "If one watches the time which freshly-drawn blood takes to coagulate, one will see that it corresponds to the time taken by the Plättchen to degenerate. Moreover, the fluids which delay or prevent coagulation (*e.g.*, carbonate of soda or of magnesia) delay or prevent the granular change of the Blutplättchen." And he further says that while the white corpuscles, at the appearance of coagulation, show no change, the "Plättchen" alter very distinctly; and that the fibrin is precipitated just where they are seen.

I can, from my own observations, fully confirm the second of Bizzozero's premises, except that I think some of the white corpuscles do seem to change and break down during the production of fibrin, and to act as centres for its production when they have broken down. It is, however, only a few of the white corpuscles that seem to do this.

Bizzozero found it very difficult to isolate the "Plättchen" from the white corpuscles, or the white corpuscles from the "Plättchen"; so he determined to try the effect of pieces of "lymph-corpuscle-holding" glands in the coagulation of "protoplasmic fluid," and to compare this with the effect of threads which had been stirred through freshly-drawn blood. To threads so prepared, there adhere an immense number of "Blutplättchen," and only a comparatively small number of white corpuscles; but, according to Bizzozero, so many of the latter do adhere that it is quite impossible from experiments with such

¹ Alex. Schmidt, *Archiv f. die gesammte Physiol.*, xi. (1875), p. 291.

threads alone to say whether it is the "Blutplättchen" or the white corpuscles that cause the coagulation.

For "lymph-corpuscle-holding" glands, Bizzozero employed spleen, bone-marrow, and lymphatic glands; and he found that pieces of these glands either failed to induce coagulation of the protoplasmic fluid or only induced it very slowly.

As to this observation of Bizzozero's, I may say that it does not in my opinion strengthen the position he takes up against the view held by A. Schmidt. If white corpuscles induce coagulation only after breaking down into "Plättchen," it is but natural we should not find that the most recently-formed white corpuscles, such as those found in the lymphatic glands, are active in causing coagulation; inasmuch as such corpuscles are not so likely to break down as corpuscles which have been in the circulating blood for some time. And it seems to me hardly fair to compare the effect of a piece of spleen on protoplasmic fluid with the effect of threads which have been drawn through blood, and which, therefore, contain the adhesive elements of the blood in a very concentrated form, while the white corpuscles in the spleen are diluted by the other elements of the spleen-substance. And, further, I think that when Bizzozero mentions the spleen and the bone-marrow, he forgets that in the recent state a very large part of the volume of each of these organs is made up of the blood contained in its venous sinuses and in the meshes of its pulp, and that this blood must contain as many of the "Plättchen" as the circulating blood elsewhere. His observations are, however, at any rate against the idea that the lymph-corpuscles *as such* are capable of inducing coagulation; for if they had been, pieces of lymphatic gland would certainly have been as active in producing coagulation as his threads.

As to the origin of the "Plättchen," Bizzozero expresses no opinion, beyond saying that he sees nothing to support their origin from the white corpuscles. From my own observations, however, I have been led to think that they *may* be derived from the white corpuscles, though only from a particular part of them, viz., the nucleus. They do not as a rule take origin from the nucleus of a white corpuscle, but they *may* have such an origin, when a white corpuscle breaks down, either in the circu-

lating blood or soon after the blood has left the vessels. Their *usual* origin is, I believe, the nucleus of a nucleated red corpuscle; but as the nucleated red corpuscle, as I shall later in my paper attempt to show, was once a white corpuscle, the *occasional* origin of these "Plättchen" direct from a white corpuscle seems not unlikely.

I have paid very particular attention to the so-called new elements in the blood, both in fresh preparations of the blood and in preparations diluted with artificial serum (I used sodium-sulphate solution of sp. gr. 1022), and I entirely agree with Neumann and other writers in considering that the "Körnchenbildungen" are neither fresh elements nor young blood-corpuscles. I do not, however, entirely agree with Neumann as to their origin. He, as already mentioned, looks on them all as **broken-down red corpuscles**.—As to the "Blutplättchen" of Bizzozero, I am inclined to think them identical only with one variety of the "Körnchenbildungen."

I have satisfied myself that in the blood after it is drawn, there are, in addition to the red and white corpuscles, two distinct elements; and I am convinced that one of these elements is derived from the breaking-down of the red corpuscles, while I think it very likely that the other is derived from the nucleus of young red blood-corpuscles, or, occasionally, from the nucleus of white corpuscles.

In a paper which I wrote on the "Invisible Blood-Corpuscle of Norris,"¹ I said that I did not consider the "Blutplättchen" of Bizzozero to be identical with Norris's corpuscles, and that I was much more inclined to look on the "Plättchen" as portions of white corpuscles, derived from the white corpuscles as they were breaking down to liberate the fibrin ferment. That my views on this latter point have since become modified will be understood from what I have already said.

As the various names I have mentioned as being applied to these elements have been used somewhat vaguely, I shall discard them, and employ as a general term the old name "microcyte:" simply distinguishing into *coloured* and *colourless microcytes*.

(a.) The *coloured* microcytes.

¹ *Jour. of Anat. and Physiol.*, July 1884.

These are simply fragments of broken-down red corpuscles ; and any one who takes the trouble to watch a preparation of blood for a sufficient length of time will notice, first that the red corpuscles become crenated,—some much more quickly than others,—and then that the so-formed thorn-like processes become broken off, and float away as rounded or sometimes oval bodies,—the remains of the corpuscle being left behind as an irregular coloured body. They are, I believe, the bodies which Neumann looks on as the “*hæmatoblasts*” of Hayem ; as I cannot suppose that Neumann attributed the presence of the other variety of microcyte in the blood to the breaking-down of the red corpuscles. And I further think that they are looked on by Hayem as *one stage* in the life-history of his “*hæmatoblasts*.” For, of course, all kinds of intermediate forms can be observed, between the smallest of the coloured microcytes and the red corpuscles ; though to account for Hayem’s opinion that his “*hæmatoblasts*” are derived from the lymph-corpuscles, it would be necessary to bring in the second, or colourless variety of microcyte.

(b.) The *colourless* microcytes.

These are the “*Blutplättchen*” of Bizzozero.

If a drop of blood be taken on a slide and be covered and examined very quickly, there are seen brightly refractile oval or rounded bodies, varying from 1 to 3 micros. in diameter. These bodies are at first isolated ; are adhesive, *i.e.*, tend, like white corpuscles, to adhere to the slide and to the cover-glass ; and refract light in the same peculiar way as white corpuscles. Very quickly they mostly run together to form groups, in which the individual members of a group can at first be distinguished, though they soon fuse into a common finely-granular mass (“*Körnchenhaufen*”). Those which remain isolated also become irregular and finely granular.

At first, I was very much inclined to look on these microcytes as fragments of the perinuclear part of white corpuscles ; and certainly the longer they are of being examined after the blood is drawn, the more are they like the perinuclear substance of the white corpuscles. I never, however, could quite satisfy myself on this point ; although I found, in preparations of blood diluted with sodium-sulphate solution, appearances which would very much support my view. As everyone knows, solutions of

the neutral salts of sufficient strength prevent coagulation of the blood. I found that the solution of sodium sulphate which I used for diluting the blood for the purpose of examination prevented the alteration of the colourless microcytes. (Bizzozero, who also observed this, noted that the solution was still more preservative if it contained a little methyl-violet.) In preparations of the blood thus diluted, I could examine these microcytes and compare them with the white corpuscles. In these preparations, I often found what appeared to me to be a white corpuscle partially broken down and with a few microcytes lying near it; and I was inclined to think that these were instances of white corpuscles caught and fixed in the act of breaking down into microcytes. But in undiluted blood, although I could see individual examples of white corpuscles breaking down and producing bodies like the colourless microcytes, still it was always only some time after the blood had been drawn, and during the stage of fibrin production. The fragments of the white corpuscles then broken off were like the condition of the microcytes at that period, *i.e.*, finely granular; but not like the first condition of the microcytes. And, further, I could not account for the very large number of colourless microcytes sometimes found in the blood; as it was hardly possible to suppose that the white corpuscles broke down into microcytes so rapidly that they had all broken down before the preparation could be put under the microscope. Nor could I account for Bizzozero's finding them in the circulating blood. And yet, in spite of being unable to explain everything, I could not give up the idea that the colourless microcytes were derived from the white corpuscles.

Now, however, I think I have found a better explanation of their origin. Further observations will have to show whether I am right or not; but I advance my opinion with very strong hopes of its being correct.

In treating a preparation of blood with $\frac{1}{2}$ per cent. solution of acetic acid, I caused the white corpuscles to swell up, and the nuclei of some of them struck me in a way they had never done before. As is well known, white corpuscles so treated show more than one nucleus, generally from 3 to 5 or 6; and in my preparation these nuclei, separated from each other by the

action of the acetic acid, had exactly the appearance of the colourless microcytes. The resemblance, indeed, struck me so forcibly that I at once began to speculate as to whether the microcytes could be derived from them; and I found that many facts could be brought forward which would support such an origin. Moreover, I saw that if the nuclei of the white corpuscles may be the forerunners of these microcytes, then the nuclei of the nucleated red corpuscles may also be so; and I think it is chiefly as the divided nuclei of the nucleated red corpuscles that these microcytes are to be regarded. I have not myself made sufficient observations on the changes of the nuclei in the nucleated red corpuscles to be able from them alone to say whether such nuclei break down into bodies similar to these microcytes; but both Kölliker and Neumann have from their observations come to the conclusion that the nucleus of a nucleated red corpuscle does break down into small pieces. Neumann¹ evidently *thinks* that these small pieces become absorbed in the general substance of the cell. Kölliker² says that this appearance of a broken-down nucleus is specially well seen after the action of acetic acid, and that the nucleus of a nucleated red cell is very apt to break down under the influence of weak acetic acid.

Further, with reference to the comparison of nuclear changes in nucleated red corpuscles with nuclear changes in white corpuscles, I have to say that, judging from the general appearance of white corpuscles without the addition of a reagent, I am very far from thinking that there are really so many nuclei in white corpuscles as after the addition of acetic acid there appear to be. It seems to me much more likely that their multi-nuclear condition after the addition is due to the action of the acid on a previously perhaps single nucleus, causing it to break down.

After the nucleus of a nucleated red corpuscle has served its function in enabling the cell to assume hæmoglobin (for this I believe, and later in this paper shall try to show, to be the function of the nucleus in the early stage of the red corpuscle), it is of no further use, and disappears from the cell. The way

¹ Neumann, *Archiv d. Heilkunde*, Bd. xv. p. 459.

² Kölliker, *Mikrosk. Anatomie*, Bd. ii. p. 590.

in which it disappears is disputed: Kölliker and Neumann saying that it falls to pieces; and Rindfleisch¹ contending that, surrounded by a small amount of undifferentiated protoplasm, it passes bodily out of the cell. Putting together the observations of Kölliker, Neumann, and Rindfleisch, and considering these observations with regard to their bearing on the colourless microcytes, I am inclined to think that the nucleus both breaks down and passes out of the cell: that is, that it first breaks down as it does after the influence of acetic acid; and that these portions then pass out of the cell, leaving it a non-nucleated red cell. These portions of the nucleus are, I believe, the colourless microcytes which have been seen by Bizzozero in the circulating blood, and by everybody else in the blood after it has been drawn.

That the colourless microcytes are the agents which immediately induce coagulation, and which probably take part in the formation of fibrin, I hold to be capable of the clearest proof. Not only the observations of Bizzozero himself, but also those of Schmidt and others, who look on them as broken down white corpuscles, are in favour of this action of the microcytes; and as it is an action which I have frequently seen under the microscope, there is, in my opinion, very little room for doubting it. Those microcytes which remain single can be seen to become granular, and threads of fibrin can be seen stretching out from them as centres; they, at first, forming the nodes of the fibrin network, but ultimately seeming, partially at least, to disappear in it. The groups of microcytes behave in exactly the same way.

Although, like Bizzozero, I have been unable to see the great breaking down of white corpuscles which Schmidt describes, I cannot agree with Bizzozero, when he says that none of the white corpuscles suffer a change during the formation of fibrin. A few of them appear to me to break up; and around those that break up an active precipitation of fibrin appears to occur, just as around the microcytes and groups of microcytes. And this does not at all form an objection to my idea of the origin and function of the microcytes: for, in breaking up, the white corpuscle exposes its nucleus, which probably also breaks

¹ Rindfleisch, *Archiv f. Mikrosk. Anatom.*, Bd. xvii. pp. 21-42.

up into pieces and goes through the same changes as the microcytes.

The reasons which lead me to suppose that the colourless microcytes are derived from nuclei of blood-corpuscles, and especially from those of the nucleated red ones, are the following :—

1. The great similarity in appearance between the fragments of the nucleus of a white corpuscle after the addition of acetic acid and the colourless microcytes; and also the exactly similar appearance and refraction which the microcytes have to white corpuscles which have not been acted on by reagents, and more especially to the central part of such corpuscles.

2. The similarity in the manner in which the fragments of the nucleus of a white corpuscle and the colourless microcytes stain. When the fragments of the nucleus are separated, they stain with methyl-violet only very slightly; and the colourless microcytes when separate also stain only very slightly. And, again, when the fragments of the nucleus are accumulated together, as in a perfect nucleus, they stain darkly; and, in the same way, groups of the colourless microcytes seem to take up the dye very distinctly indeed.

3. A fact observed by Neumann, and also frequently by myself: that when the nucleus of a nucleated red corpuscle is under the influence of acetic acid broken up into fragments, it then becomes coloured by hæmoglobin, which has diffused out of the body of the corpuscle. To which may be added, that I have observed that if blood be mixed with a solution of a neutral salt, so as to prevent the colourless microcytes from changing, these then, *after a time*, become faintly coloured by hæmoglobin, which has diffused out of the red corpuscles,—a behaviour which has, I think, been one reason why Hayem describes them as faintly hæmoglobin-tinted.

4. The fact that Kölliker and Neumann have seen the nuclei of the nucleated red cells in different stages of breaking down. Neumann has, in fact, seen cells with only one fragment of the nucleus left, the rest of the nucleus having (according to my idea) passed out of the cell. I have seen similar appearances myself, but have not made sufficiently exact observations to be able to speak definitely.

5. Which I think a most important point, and one which, besides having been noted and recorded by Bizzozero and others, has also been observed by myself, viz., that the more active the blood-forming process, and consequently the greater the number of nucleated red corpuscles found in the blood-forming organs, the more numerous are the colourless microcytes found in the blood. (Concomitantly with this increase in the number of microcytes, I have observed a very marked increase in the tendency of the blood to coagulate.)

To return to Hayem and Pouchet, inasmuch as they describe under the name of "hæmatoblasts" (Hayem) or "globules of Donné" (Pouchet), (1) colourless elements, which Hayem at least supposes to be derived from the white corpuscles, and (2) elements which are somewhat larger and are coloured by hæmoglobin, and which they suppose to be transition stages between the colourless variety of elements and the full-sized and colourless hæmocyte, I am driven to conclude that, in describing their hæmatoblasts, they have included both the colourless and the coloured microcytes, and have supposed the colourless microcytes ("Blutplättchen" of Bizzozero) to be the first stage, and the coloured microcytes later stages, of elements which, according to them, develop into the ordinary non-nucleated red corpuscle of mammalian blood.

With regard to the *fourth* variety of element said to exist in the blood, I need not say much. The elements in question are the "invisible blood corpuscles of Norris." Concerning these corpuscles, I published a paper in the *Journal of Anatomy and Physiology* for July 1884, in which, without pretending to say whether "invisible" corpuscles do exist in the blood, I disputed, I think conclusively, the chief methods by which Dr Norris says he has brought them into view. My further observations on the blood all go towards supporting the opinion I expressed in that paper, viz., that the "invisible corpuscles" of Norris are simply decolorised red corpuscles.

(To be continued in the next Number.)

ON THE RELATIONSHIP OF UREA FORMATION TO
BILE SECRETION: AN EXPERIMENTAL RESEARCH.¹ By
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PART I.—PRELIMINARY.

THE relationship of the liver to the elimination of the effete nitrogenous matters of the animal body is a subject of the greatest physiological interest, and also of prime practical importance. It has arrested the attention of many of the ablest physiologists, each one of whom has added something to our knowledge of the subject, but none of whom can be said finally to have settled the question of the precise nature of the relationship of the liver to the production of urea.

In order further to elucidate this subject, I have undertaken the following research, in which I have endeavoured to ascertain whether the excretion of urea bears any relationship to the secretion of bile.

For this purpose I have investigated the influence on the urea excreted by the kidney of the more active of these substances, which have been shown by Rutherford (*Trans. Royal Society of Edinburgh*, vol. xxix.) to have a special action in stimulating the biliary function of the liver.

Evidence of any kind on this subject must be of importance, for, if negative, it must indicate that the biliary function of the liver at least is not connected with urea production; while, if positive, a most decided step in the physiology of urea formation is thereby made.

For this investigation I have selected the following drugs:—salicylate of soda, benzoate of soda, colchicum, perchloride of mercury, and euonymin—drugs representing different pharma-

¹ This Paper formed part of a Thesis presented to the Medical Faculty of the University of Edinburgh, May 1883, for graduation as Doctor of Medicine, and for which a Gold Medal was awarded to the author.

cological groups, and differing widely from one another in their general physiological action, but all agreeing in being powerful stimulants of the biliary function of the liver.

The practical importance of such a research is considerable, for the somewhat empiric use of certain of these drugs in gout, rheumatism, diabetes, and other diseases in which the tissue metabolism is gravely affected, should, by such an investigation, be rendered more rational and scientific. For this reason I have also studied the changes produced in the excretion of uric acid under the administration of these drugs.

Before giving the results of my own experiments, it will, however, be necessary briefly to refer to the evidence we already possess in regard to the connection of the liver with urea formation.

The literature on this subject is enormous, and in discussing it I shall, instead of following a chronological sequence, attempt to arrange the information we possess in such a way as to render as clear as possible the extent of our present knowledge.

Three theories have been advanced in regard to the locality of the formation of urea,—(1) that it is produced in the kidney; (2) that it is produced in the muscular system; and (3) that the liver is the seat of its production.

That the kidney is in any sense the seat of its production has been long ago disproved. Prevost and Dumas (*Annal. de Chim. et de Phys.*, t. xxiii. p. 116) were the first to show that, after extirpation of the kidneys, urea was to be found in large quantities in the blood. And this observation has since been confirmed by Marchand, Voit, Meissner, and others, while the observations of Petroff (*Virch. Arch.*, Bd. xxv. S. 91), of Zalesky (*Untersuchungen ü. den Urämischen Process und die Function der Nieren*, 1865), and of others, that after ligature of the ureter the increase in urea is greater than after extirpation of the kidney, cannot be considered as indicating the production of urea in these organs, since it must be remembered that the animal survives this less grave operation for a much longer time, and that thus a more extended period is allowed for the urea to accumulate. In addition, vomiting is not so frequently induced, and Claude

Bernard has shown that in this way the urea already accumulated in the blood may be got rid of.

The question of the relationship of the kidney to urea production has also been investigated by the transfusion method of Ludwig. Gréhant (*Cbt. Med. Wissensch.*, 1870, p. 249) has shown that there is less urea in the blood flowing from the renal vein than is contained in the blood entering the organ; while von Schröder (*Arch. f. Exp. Path. u. Pharmac.*, xv. p. 364) shows that, even when carbonate of ammonia is added to the blood, no production of urea occurs during its circulation through the kidneys.

The recent experiments of Abeles (*Wiener Acad. Sitz.*, iii. Abth., Bd. lxxxvii. p. 187) on transfusion of the kidney do not bear upon this subject, and simply show that urea is separated from the blood by the renal epithelium.

Liebig's theory of the production of urea for the oxidation of the proteids in muscle, though ingenious and fascinating, was not based upon experimental evidence, and all recent works on this subject tend to show that the muscles are not the source of urea.

The older investigations, as those of Meissner and Picard, on the presence of urea in muscular tissue, are rendered valueless by the faulty methods employed for the determination of the urea. But recently Haycraft, using his own admirable method for the estimation of urea (*Jour. of Anat. and Phys.*, vol. xvii.), has finally demonstrated that only the smallest trace of urea is to be found in muscles, and that the quantity is not increased after violent exercise. He has further demonstrated that the blood does not gain urea after violent exertion, while von Schröder (*loc. cit.*), Gréhant et Quinquand (*Gaz. hebdom. de Med. et de Chir.*, 1884, No. B.), and Salomon (*Virchow's Archiv*, vol. lxxix., 1884, p. 149), have all proved experimentally that no increase in the urea occurs in blood circulating through muscles at rest, even when carbonate of ammonia is added.

It is impossible here fully to discuss the much vexed question of the influence of muscular exertion in the nitrogenous excretion by the kidneys; but the subject is ably dealt with in Gamgee's *Physiological Chemistry*, vol. i. p. 385. Undoubtedly

the mass of evidence goes to show that during muscular exertion, especially when this is severe, an increased excretion of urea *may* occur. This is always small, and not at all in proportion to the work done, and it must be remembered that such an increase by no means indicates that the nitrogen so excreted is really derived from the muscles, for, concomitantly with all muscular effort, we have changes occurring in all the organs of the body. Such a method of research must be considered as highly unsatisfactory.

The last probable place of urea formation is the liver, and upon this subject the evidence is somewhat conflicting.

No less an authority than Hoppe-Seyler denies the occurrence of urea in the liver (*Zeitsch. f. Physiol. Chem.*, Bd. v. p. 348). A brief note to all that is given, and no theory is advanced as to the nature of the "syrupy base gradually becoming crystalline," which he describes as occurring in the organ.

Other observers state positively that it does occur in the liver; but while Meissner (*Zeitsch. f. rat. Med.*, Bd. xxxi.) and Gscheidlen (*Studien über den Ursprung des Harnstoffs im Thierkörper*, Lepsig 1872) admit that the percentage amount is at least not greater than that contained in the blood, Munk (*Pflüger's Archiv*, Bd. ii. S. 41) concludes that the percentage amount is really smaller.

A method of research which has in the hands of many observers yielded important results is the "durchströmung" method of Ludwig, which consists in transfusing blood through the fresh organ kept at the temperature of the body in a warm chamber. In connection with the liver this was first employed by Cyon, who briefly records two experiments in the *Obt. f. Med. Wissen.* 1870, p. 580. He finds that blood which has passed through the liver several times contains a much higher proportion of urea than it contained before the transfusion. In his second experiment, before transfusion was commenced, 100 c.c. of blood contained 0.08 grm. of urea, while after the blood had circulated through the organ eight times it contained 0.176 grm. Unfortunately Cyon's method of estimating urea in the blood was essentially bad, as no precautions were taken to prevent other extractives besides urea being precipitated by the mercuric nitrate used in his process.

Gscheidlen (*loc. cit.*) discusses Cyon's experiments, and from his own observations he comes to the conclusion that the increase in the amount of urea which Cyon demonstrated is really due to a washing of that substance out of the liver tissue. His experiments appear to have been conducted with the greatest possible care. Before the transfusion was commenced a lobe of the liver was ligatured off from the rest, so that no blood could circulate through it. The percentage amount of urea in the blood was determined before the commencement of, and at different periods throughout, the experiment, and, finally, the urea in the ligatured part and in the transfused part of the liver was estimated. I shall here quote the results of his fourth and most complete experiment, as his conclusions are of considerable importance:—

Exp. IV.

Isolation of lobe completely successful.

Weight of liver without blood, = 513 grms.

Isolated part = 133 grms. containing 0·018% urea.

Transfused part after escape of
38 grms. of blood = 380 grms. " 0·0092 "

The amount of blood used was 870 c.c.

Blood before transfusion,	. . .	1068 sp. gr.	0·020	"
" twice transfused,	. . .	1071	0·021	"
" three times transfused,	. . .	0072	0·0272	"
" four	" . . .	1077	0·041	"

The absolute amount of urea at the beginning of the experiment in the liver weighing 513 grms., was 0·0923 gm., so that, after subtracting 0·0239 gm. contained in the ligatured portion, there remained in the transfused part 0·0684 gm., and at the end of the experiment 0·0349 gm., so that 0·0349 gm. were washed out.

Thus stated, his experiment undoubtedly indicates that the urea is washed out of the liver by the blood flowing through it. But if we take into account a factor which Gscheidlen appears to have overlooked, we see that an actual production of urea must have occurred during this experiment.

The 870 c.c. of blood employed contained before the experiment 0·020 per cent. of urea, that is, 0·1858 gm. of urea. After passing once through the liver, the amount of urea was 0·1956 gm., an increase of 0·0098 gm. Now, supposing that, for the purpose of analysis, 100 c.c. of blood were withdrawn for the

experiment at this time, in the second transfusion 770 c.c. of blood would pass through the liver, and at the end of this passage as much as 0.2242 gm. of urea were contained in the blood—that is, a further addition of 0.0286 gm. of urea has occurred. Allowing for the withdrawal of another 100 c.c., we have during the third transfusion 670 c.c. of blood, which at the end of the experiment contained 0.0716 gm. of urea, making in all a gain to the blood of no less than 0.1100 gm. of urea, only 0.0334 gm. of which can be accounted for by the urea washed out of the liver. Here, therefore, we have a clear demonstration of the fact that 0.0766 gm. of urea were actually formed during this experiment.

This very important piece of evidence is of special value, as Gscheidlen's whole paper is an attempt to combat experimentally the view that the liver is the organ in which urea is produced,

Von Schroöder (*Arch. f. Exp. Path. u. Pharmac.*, vol. xv. p. 364), using a very accurate method of urea determination devised and tested by himself, has investigated fully by the "durchströmung" method the production of urea in the liver. His results are as follows:—

1. That in the fasting dog no increase in the urea contained in the blood occurs after the blood has passed several times through the liver.
2. In a dog in full digestion, an increase of 27.5 per cent. was observed.
3. On adding carbonate of ammonia to the blood, a very great increase in the urea occurs—as much as 222.9 per cent. in one experiment. This increase is fairly proportional to the amount of ammonia employed.
4. In passing blood containing carbonate of ammonia through muscle no increase in the urea occurs.
5. On passing blood with ammonia through the kidney of the ox; on blood being also used no increase in the contained urea occurred.

These experiments are in every way more satisfactory than those of Cyon and Gscheidlen, and the very different results obtained in fasting and digesting animals is of special importance.

The most recent paper on this subject is by Salomon (*loc. cit.*). This observer shows that upon the addition of ammonia

a large increase in the amount of urea contained in the blood occurs during its passage through the liver, while no such increase is to be observed after circulation through the hind limb.

In regard to the presence in the blood of the hepatic vein of an amount of urea greater than is contained in the rest of the blood, Gscheidlen (*loc cit.*) and Gréhant and Quinquand (*Gaz. hebdom. de Med. et Chirurg.*, 1884, No. B.) have come to diametrically opposite conclusions. The older observer adopted an ingenious method of catheterising the hepatic vein from the right jugular view. The following table gives his results:—

Exp.	Remarks.	Carotid.	Vena Cava Inferior.	Hepatic Vein.	Vena Cava Inferior.	Right Heart.
		Per cent.	Per cent.	Per cent.	Per cent.	Per cent.
1	Flesh diet,	·022	·0217	...
2	Flesh diet,	·027	·018	·029	...
3	Ordinary diet.	·021	·023	·019	...
4	Hunger three days,	·0138	·0159	0·168	·014	...
5	Flesh diet, . .	·024	·024	0·20	...	·030

These results, if of any value, would tell against the theory of the formation of urea in the liver. The method is certainly ingenious, and the experimenter distinctly states that in every case he assured himself, by digital exploration, that the tube really was in the hepatic vein. But, recollecting the intimate relationship of the vena cava inferior to the right lobe of the liver, and at the same time recalling the great difficulty of satisfactorily exploring this part of the abdominal cavity, we are bound to confess that it is highly probable that fallacies quite sufficiently grave to account for the very discrepant results given in the table may have occurred.

Gréhant and Quinquand have more recently investigated this subject, but in the short note of their observations in the *Gaz. hebdom.* no account of their method of experiment is given. It is merely stated that these observers found a larger proportion of urea in the veins of the liver than in the systemic veins.

Perhaps the most important recent contribution to this subject is that recorded by Minkowski in the *Cbt. f. die Med. Wissensch.* for the 10th January of this year. It is a well-

known fact that uric acid in birds takes the place of urea in mammals not only in the urine, but also, as shown by Meissner, in the liver. Taking advantage of the fact that the vena Jacobsonii, which connects the portal vein with the veins of the kidney in nearly all birds, is, in the goose, specially well developed, he excluded the liver from the circulation both by ligaturing its vessels and by excision, and found that the uric acid normally occurring in the urine was replaced by lactic acid. This experiment clearly demonstrates that in birds uric acid is produced in the liver, and renders it highly probable that in mammals urea is produced in the same organ. Of especial interest are these observations of Minkowski, when we recall Frerich's discovery of the disappearance of urea and appearance in its place of leucin and tyrosin in acute yellow atrophy of the liver.

Besides these strictly scientific methods of investigating this question, other modes of experiment have been employed. Among these *Electrisation of the Liver* has yielded in the hands of Sigrist (*St Petersburg. Medic. Wochsch.*, v. Jahrg., 1880, Nov. 12) and of Stolnikow (*ibid.*, 1870) positive results. I have been unable to procure the original papers, but Saenger, whose investigations on this subject must be mentioned later, gives a full abstract of the former observer's work. In five experiments the interrupted current was employed, and in two the constant current. In all one electrode was placed just under the ensiform cartilage, while the other was moved about over the surface of the liver, care being taken to avoid causing muscular contractions. The urea excreted by the kidneys was estimated daily. In all seven cases a well marked increase in the urea was observed during the days upon which electricity was used, and after the cessation of this treatment a return to the normal occurred. Stolnikow (*loc. cit.*) finds a similar increase both with men and dogs. Saenger (*Ueber die Harnstoffausscheidung nach Electricisirung der Leber*, "Inaug. Dissert.," Göttingen, 1881), employing the same mode of stimulation as Sigrist, finds absolutely no increase in the urea excreted. His observations were made on patients attending the eye clinique who were free from internal disease. The diet consisted of black bread with butter, about 200 to 250 grms. of flesh,

vegetables, potatoes, and milk soup. Five experiments are recorded, and in none of these is there any rise in the urea excreted, though the water of the urine is very markedly increased in amount.

The evidence afforded by electrical stimulation of the neighbourhood of the liver is therefore so conflicting that it must be disregarded.

M. Bronardel (*Arch. de Phys.*, 1876) gives one extremely interesting experiment upon the influence on the urea excretion of artificially produced congestion of the liver of a dog. His mode of experiment was as follows:—A small dog was kept for some time upon fixed diet, the urine was daily collected and measured, and the urea estimated by the hypobromite process.

When the urea excretion became fairly constant, the dog was held up and the region of the liver was violently beaten with a stick. The following table shows the result of this experiment:—

Date.	Urine.	Urea.	Remarks.
July 14	300	12·10	Contusion of liver.
„ 15	200	13·80	
„ 16	200	9·00	
„ 17	150	9·00	
„ 18	320	31·50	
„ 19	280	21·80	
„ 20	400	32·00	
„ 21	200	16·00	
„ 22	200	17·10	
„ 23	320	18·90	
„ 24	500	22·00	
„ 25	320	17·20	
„ 26	200	16·00	

He observes that the appetite of the dog remained good during the whole experiment.

Striking as are the results obtained, such an experiment is by no means free from objections. In the first place, one such observation is not sufficient; in the second place, we have no evidence that the liver really was congested; and, in the third place, it would be necessary to show that a contusion elsewhere will not produce a similar result. For Angerer (*Klin. u. exp.*

Unters. über die Resorb. von Blutextravasat., 1879) has shown that the production of a hæmatoma will induce a well-marked degree of fever lasting for some days, and, therefore, especially when we remember that it is connected with resorption of blood, may in itself be sufficient to account for the increased urea formation.

Passing now to the consideration of the clinical evidence on the subject, our attention is at once arrested by the important discovery of Frerichs concerning the changes in the urea excretion during the progress of acute yellow atrophy of the liver. His observations are so generally known that it is needless to reproduce them here. The diminution and ultimate disappearance of urea from the urine, its place being taken by leucin and tyrosin, during the course of this atrophic disease of the liver, is a fact of prime importance. To quote Salkowski's observations on the subject—"Das Gewicht dieses Factum kann durch gegentheilige physiologische Experimente nicht erschüttert werden."

Less well known than Frerichs' observation, but nevertheless of very great importance, is the long series of experiments recorded by M. Bronardel (*loc. cit.*), from which he contends that the amount of urea excreted depends upon—

1. The state of the hepatic cells.
2. The greater or less activity of the hepatic circulation.

It is impossible here to discuss at length his long and exhaustive paper. His chief conclusions are as follows:—

1. In ictère grave (acute yellow atrophy) the urea is diminished, and may entirely disappear.
2. In the ictérus of phosphorous poisoning the urea diminishes considerably, but after each injection of the drug a rise in the amount is observed.
3. In ictère pseudo-grave the urea behaves in the same way as in ictère grave, but at the urinary crisis a considerable elimination of urea occurs, and at the same time the liver augments in size.
4. In simple ictérus the urea is not diminished; it may be increased.
5. In suppurative hepatitis, according to Parkes, the urea is increased in the early stages, but it is diminished when the abscess has destroyed liver tissue.

6. Biliary calculus, followed by atrophy of the liver, is connected with diminution in the urea. This diminution is best marked during the hepatic colic. Also, according to Reynard, it is diminished in intermittent hepatic fever.
7. In cirrhosis of the liver, whether it be hypertrophic or atrophic, the urea is diminished even though the patient continues to take much food.
8. In heart disease the urea is diminished.
9. In phthisis, &c., urea is diminished.
10. It is similarly affected in chronic hepatic affections, as cancer, &c.
11. In congestion of the liver the urea is increased.
12. In lead colic it is diminished, but it increases in amount as the liver increases in size.
13. In transient glycosuria the urea increases along with the glycosuria, or just as it is disappearing.
14. In diabetes there is a great increase in the urea.

So much for the clinical evidence, which points even more strongly than the experimental to the liver as the seat of urea formation.

Reviewing as a whole the facts here given, we are forced to the conclusion that, though we have no evidence that urea is produced or is contained in the liver cells, no doubt can exist that the blood in passing through the liver gains urea, and that this increase in the urea depends directly upon the condition of the hepatic cells.

In a future paper I intend to record the results of an investigation undertaken to elucidate the question of how this increase is brought about. At present I shall confine myself entirely to the relationship of the production of urea with the secretion of bile.

(To be continued in the next Number.)

THE INDEX OF THE PELVIC BRIM AS A BASIS OF
CLASSIFICATION. By Professor WM. TURNER, M.B.,
LL.D., F.R.S.

[This proposed classification of the pelvis was communicated to the Anthropological Section of the British Association in Aberdeen, September 1885. It forms a part of the chapter on the pelvis in my "Report on the Bones of the Skeleton" collected during the voyage of H.M.S. "Challenger," and the Tables of Measurements referred to are included in that Report.]

THAT the inlet to the true pelvis presents variations in outline, and in the relative proportions of its conjugate and transverse diameters, has been recognised by anatomists since the form of the pelvis in the different races of men began to be studied. Thus Vrolik pointed out¹ that in the Negro the conjugate diameter of the brim was very great in proportion to the transverse diameter when compared with the European. But the first to put these variations into systematic shape was Professor M. J. Weber of Bonn, who described four prime forms of pelvis, which he designated oval, round, four-sided, and wedge-shaped.² In the oval pelvis the transverse diameter of the brim distinctly exceeded the conjugate, and the pelvic inlet was transversely ovoid; in the round pelvis the transverse and conjugate diameters were almost equal, and the pelvic inlet was circular; in the four-sided pelvis the transverse diameter exceeded the conjugate, the sides and anterior and posterior boundaries of the pelvic brim were flattened so as to give a quadrangular shape; in the wedge-shaped pelvis the inlet was laterally compressed, and the transverse diameter greatly reduced near the symphysis, so that the pubic bones joined at an acute angle, the conjugate diameter was therefore greater than the transverse, and the outline of the inlet was cuneiform. Although he recognised that differences existed in the dimensions of the conjugate and transverse

¹ *Considérations sur la Diversité des Bassins de différentes races humaines*, Amsterdam, 1826.

² *Die Lehre von den Ur- und Rassen-formen der Schädel und Becken des Menschen*, Düsseldorf, 1830.

diameters in the same pelvis, yet Weber did not give such a numerical expression to these differences as to enable them to be referred to a common standard. A few years afterwards von Stein divided¹ the form of the pelvic inlet into four classes—truncated-cordate (abgestumpfte Kartenherzform); elliptical, where the transverse diameter is the larger; round; and elliptical, where the conjugate diameter is the larger. He stated also that one would be justified in speaking of a difference of breadth index in the pelvis as in the skull. Like Weber he does not appear, however, to refer these differences to a common standard. This was, however, subsequently done by Professor Zaaier of Leyden, who, in his important memoir on the form of the pelvis in the women of Java,² suggested that, in order to give a fixed standard of comparison between the conjugate and transverse diameters, the transverse diameter should be regarded as equal to 100. Then by multiplying the conjugate diameter by 100, and dividing by the transverse diameter, the proportion which the conjugate diameter bore to 100, or in other words a pelvic or brim index, was obtained. When these diameters bore to each other the relation of 100 to 90 or under, then he regarded the pelvic inlet as round. But when the conjugate was greater in relation to the transverse, he called it longish oval. About the same time C. Martin grouped³ pelves into *a*, those with a round inlet, in which the conjugate was almost as large as the transverse diameter, or at the most one-tenth smaller; and *b*, those with a transversely oval inlet, in which the conjugate was more than one-tenth smaller than the transverse diameter.

The mode of estimating the brim or pelvic index after the the formula of Professor Zaaier has been adopted by the majority of anthropologists, though some would have preferred to have reversed his formula and to have taken the conjugate diameter as equal to 100.⁴ This, indeed, was at one time the

¹ "Ueber die Meinung von Racenverschiedenheiten der Becken," *Neue Zeitschr. f. Geburtskunde*, Bd. xv., 1844.

² *Holländische Gesellschaft der Wissensch. zu Haarlem*, D. xxiv., 1866.

³ "Beckenmessung an verschied. Menscheurassen," *Monatschrift für Geburtsk.*, 1866, p. 23.

⁴ See for example Carl Martin's paper in *Corresp. Blatt der deutsch. Gesellsch. f. Anthro. Ethn. u. Urgesch.*, Marz, 1881.

opinion of M. Topinard, though in his *Elements d'Anthropologie générale* he has conformed to the usual practice.

The attempts which were made by Zaaier and Martin to frame a classification of the pelvis on modifications in the relative proportions of the conjugate and transverse diameters of the brim were not successful, and did not find much favour amongst anthropologists, so that one meets with but little reference to them in current literature. This failure is, I think, in a great measure to be accounted for partly by the paucity of the observations, but mainly because they based their calculations largely on the study of female pelves, in which, for sexual reasons, there is to a considerable extent an approximation in form in different races, so that one does not meet in them with such striking variations in shape as when one compares the males in the same races. In the males, therefore, the form characteristic of the race is more fixed, and from their study it is, I think, possible to frame a classification of the pelvis.

There are two groups of measurements which, from their importance, might serve as a basis for such a classification, viz., *a*, the breadth and height of the entire pelvis, from which a breadth-height index can be computed; and *b*, the conjugate and transverse diameters of the pelvic brim, from which the so-called pelvic index can be computed. There can, I think, be little doubt that, if sufficiently reliable data are obtainable, a classification of the pelvis into readily recognisable groups would be extremely convenient, and would save much time and trouble in description. Craniologists must be for ever grateful to Anders Retzius for his grouping the skulls of the races of men into the two great divisions of dolichocephalic and brachycephalic, whilst the separation from the more extreme forms of these groups of an intermediate or mesaticephalic division by Paul Broca has been of material service.

Owing to the paucity of pelves in our museums, as compared with the number of crania of the best known races, we are not in a position to speak with so much certainty of the characteristic pelvic form as we are of the head form in so many races, but there is now, I think, sufficient material belonging to a number of races to enable me to offer for the consideration of anthropologists a classification which may, I trust, be regarded as satisfactory.

The dimensions which I shall take as presenting, in my judgment, the most reliable data for comparison are the conjugate and transverse diameters of the pelvic brim, and the classification will be based on the modifications in the value of the brim index, the so-called pelvic index. I shall not, however, as was done by Zaaizer and Martin, limit myself to a division into two groups, but shall make three divisions, two of which will represent extreme forms in opposite directions, whilst the third will be intermediate. I shall express these divisions in terms derived from the Greek, so that the nomenclature in pelvic classification may be as far as possible on the same lines as the well-known divisions of crania. As the word *πέλλα* or *πέλλις* is equivalent to the Latin *pelvis*, I shall combine this word with *δολιχός*, long, to express one extreme form, with *πλατὺς*, wide, to express the opposite form, and with *μεσαίτατος*, middlemost, to express the intermediate condition. By *dolichopellic* is to be understood a pelvis in which the conjugate diameter of the brim is either longer than the transverse or approaches closely to it; by *platypellic* a pelvis in which the transverse diameter of the brim greatly exceeds the conjugate; by *mesatipellic* a pelvis in which the transverse diameter is not so greatly in excess of the conjugate.¹ It may not be possible in the present state of our knowledge to fix definitely the numerical limits of each group, as it may need a wider range of material for comparison, both as regards races and the number of pelves in each race, than we at present possess. In any case, indeed, just as in the classification of crania, the numerical limits would be arbitrary; still it will be advisable to give to each division such a range as will in all probability include within it those pelves in a given race that present the characteristic form. For the present, then, we will assume that pelves with a brim index above 95 are dolichopellic, that those with a brim index below 90 are platypellic, whilst

¹ Kilian, in an essay entitled "Das Stachelbecken," employs the term *Akanthopelys* (*pelvis spinosa*) to designate a pelvis in which the ilio-pectineal line has a knife-like edge, or a distinct pointed process projecting from it (see his *Schilderung neuer Beckenform*, Mannheim, 1854). I have not followed him in his rendering of the Greek word for pelvis, but have constructed the form used in the text. Again, I have not used the word "brachypellic," as I wished to bring out, by the employment of "platypellic," that relatively great *width* was the characteristic feature of this form of pelvic brim.

those whose brim index ranges from 90 to 95, both inclusive, are mesatipellic. But it is quite possible that these limits may subsequently need some modification.

First, we will inquire into the value of the brim index in Europeans, and about them we are fortunate to possess a good deal of information, as the dimensions of the brim have been measured in numerous pelves in several of the principal nations. Thus, if we take British pelves and reduce the measurements from inches to millimetres, we find that of those measured by J. J. Watt the males had a transverse diameter of 116 mm. (4 in. 6 lines) and a conjugate of 102 mm. (4 in.), which gives a brim index 87.9; the females, again, had a transverse diameter 142 mm. (5 in. 6 lines), and a conjugate 124 mm. (4 in. 9 lines), giving a brim index 87.3. The pelves measured by John Wood¹ gave for the males—transverse 120 mm., conjugate 103, the brim index being 85; and for the females—transverse 132 mm., conjugate 114, the brim index being 86. My own measurements of six males gave a mean transverse diameter 127 mm. and a mean conjugate 98 mm., with a brim index 77; and of eleven females a mean transverse of 137 mm. and a mean conjugate of 109 mm., with a brim index 79. M. Verneau,² in his table of the measurements of Europeans, presumably French, states that this index is 80 in the men and 78 in the women. Gegenbaur gives the mean dimensions of the brim in pelves presumably German as follows:³—for the males—transverse diameter 128, conjugate 108, the brim index being 84; for the females—transverse diameter 135, conjugate 116, the brim index being 85.9. W. H. Flower states that his measurements of 11 European males—the nation not being specified—gave a pelvic index 81, and of 14 females an index of about 78. In the measurements made by John Wood, Gegenbaur, and myself, the brim index in the male pelvis is a little below the brim index in the female, but in those measured by J. J. Watt, Verneau, and Flower, the brim index of the males somewhat exceeded the females. Additional observations on the pelvic brim in European women have been made by Garson, whose measurements give 80 as the brim index; by Navas, whose

¹ Article "Pelvis" in Todd's *Cyclopædia of Anat. and Phys.*, v., 1859.

² *Le Bassin dans les Sexes et dans les Races*, Paris, 1875.

³ *Lehrbuch der anatomie des Menschen*, p. 265, 1883.

measurements of Spanish women furnish a brim index 81; and by C. Martin, whose measurements give 69 as the brim index of Irish women, and these also are platypellic. The lowest mean recorded in any of these European nations was 77 for the males in the Scottish pelvis, and 69 for the females in the Irish pelvis; and the highest mean was 87.9 for the males and 87.3 for the females, so that they all fall into my platypellic division.

In placing the European pelvis, both male and female, so far as it is represented by these nations, in the platypellic division, it is not of course to be understood that no individual European pelvis ever attains a brim index of 90 or upwards, but that the mean in both sexes is below 90, and as a rule is markedly below that number.

In the next place, I shall speak of another type of pelvis, and shall begin by considering the brim index in the Australian pelvis. All the anatomists who have written on the characters of the male pelvis in this race agree in stating that the pelvic brim is narrow in its transverse diameter as compared with the conjugate. Professor Huxley,¹ who was one of the first, if not the first, to give a numerical expression to these diameters in this race, gives the mean pelvic index of five males which he had measured as 101, and of one female as 37. In only one of these males was the transverse diameter in excess of the conjugate. In Ecker's Australian male the index was 100, in Keferstein's 95, and the mean index of the five Australian males in the Blumenbach collection, as measured by Spengel, was 92.² In the single male Australian measured by M. Verneau the brim index was 98, and the mean of this index in two females was 80. Professor Flower,³ in his account of the osteology of the Andaman Islanders, incidently mentioned that ten male Australian pelvises which he had measured, and which probably included the five pelvises previously measured by Professor Huxley, and that measured by Dr Barnard Davis, gave an

¹ "Notes on the Human Remains" in *Laing's Prehistoric Remains of Caithness*, 1866.

² Spengel's measurements of pelvises in the Blumenbach collection are given in the Supplement to *Thesaurus Craniorum*, by Dr Barnard Davis, in a Table opposite page 96.

³ *Journal of Anthropol. Inst.*, Nov. 1879.

average pelvic index of 98. From Dr Garson's¹ measurements of five Australian female pelves an index of 91 has been computed. In my series of six adult males, measured in Table I., the mean brim index was 97, and in the only female 96; of the six males three exceeded 95, one of them very considerably so, and three were below that number.

There is now, I think, sufficient material before us to pronounce a definite opinion on the relative size of the transverse and conjugate diameters of the pelvic brim in both sexes of Australians. It is clear that in the women the transverse diameter is larger, and not unfrequently considerably larger, than the conjugate, so that the pelvic index is for the race relatively low. If we include M. Verneau's two female pelves, which, from their low index of 80, one might be disposed to doubt if they were genuine Australians, the mean index of the nine females measured was 88·5, and, if we exclude these, it was 91·3; in either case being considerably above the European mean for the same sex, and placing the Australian female pelves on the verge between the mesatipellic and platypellic groups. In the males, on the other hand, the conjugate diameter very often exceeds the transverse, and seldom falls much below it, and as the transverse diameter rapidly diminishes in the pubic region, a cuneiform pelvic brim is produced. The mean brim index of the twenty-four males measured by Ecker, Keferstein, Spengel, Verneau, Flower, and myself is 96·6, so that they distinctly belong to the dolichopellic group.

Data for enabling one to obtain a knowledge of the brim index in the Bush race have been furnished by several anatomists. The brim measurements of five males have been recorded by Johannes Müller,² Huxley, G. Fritsch,³ and myself, and of eight females by Vrolik, Müller, Huxley, Görtz,⁴ Verneau, and Fritsch. In the females the transverse diameter in some specimens considerably exceeded the conjugate, thus in Verneau's table the mean of his two pelves, one of which was the well-known Hottentot Venus described by Cuvier, gave 87 mm. for

¹ "Pelvimetry," *Jour. Anat. and Phys.*, Oct. 1881.

² *Archiv. f. Anat. and Phys.*, 1884, p. 332.

³ *Die Eingeborenen Süd Afrikas*, Breslau, 1872.

⁴ *Ueber das Becken eines Buschweibes*, Tübingen, 1868.

the conjugate and 122 mm. for the transverse diameters, with a brim index therefore of 71; whilst in the woman Afandy, described by Görtz, the conjugate was 111 mm. and the transverse 110 mm., which give an index of 100·9. The mean brim index in the eight women was 89, which places the female pelvis in the highest term of the platypellic group, though individual specimens belonged to each of the three divisions. The male Bush pelvis, again, showed a much smaller range of variation in the brim index, and the conjugate and transverse diameters were more nearly equal. The lowest index, 93, was in Fritsch's specimen, in which the conjugate diameter was 96 and the transverse 103 mm., and the highest index, 109, was in the pelvis recorded in my Table VI. The mean of the five males was 99·5, so that they have a well-marked dolichopellic character. Notwithstanding the high proportion of the conjugate to the transverse diameter, the shape of the brim, if I may judge of its form from my specimen, and from the two pelvises figured by Fritsch, is not cuneiform, for the two pubic bones do not rapidly approximate to each other as in the Australian pelvis; in my pelvis the term antero-posteriorly oval properly expresses the form of the brim.

The pelvic index of a male Hottentot, measured by Jeffries Wyman,¹ was 94·4; but the fullest information that we possess on the pelvis of the Hottentots is contained in the valuable treatise on the aborigines of South Africa by Gustaf Fritsch. He puts the dimensions of the pelvic brim of a Hottentot woman at 96 mm. for the transverse diameter and 101 mm. for the conjugate, giving a brim index 105, which is remarkably high for the female pelvis. The transverse diameter of two male Korana Hottentots is respectively 105 and 91 mm., whilst the conjugate of the same is 96 and 108 mm., from which a brim index of 91·4 for the one and 118 for the other can be computed, giving a mean for the two of 104·7. So far, then, as we can judge from these few specimens, the Hottentot pelvis is dolichopellic. Fritsch also gives the measurements of six male and one female Kaffir pelvis, and from these measurements I have calculated their indices. The female, with a transverse diameter 107 mm.

¹ *Proc. Boston Soc. Nat. Hist.*, April 1862 and Dec. 1863; also *Anthropological Review*, vol. iii., 1865.

and a conjugate 96, had an index 89·7, whilst the males varied in the brim index from 95 to 108, and had a mean of 100·6. Weber had also previously figured the pelvis of a male Kaffir, in which the transverse diameter of the brim was 3 inches 9 lines, and the conjugate 4 inches. The brim index was 102·6, and he placed this pelvis in his wedge-shaped group. There can be no doubt, therefore, that the pelvis in the male Kaffirs is dolichopellic.

A considerable number of Negro pelvises have now been measured. As a rule nothing definite has been stated, or, in all probability, indeed known of the exact districts or tribes from which most of these pelvises were obtained, but Verneau in his essay especially mentions Nubia, Mozambique, and Guadeloupe as the localities from which certain of his specimens were derived. The measurements of the Negresses described by Vrolik, Weber, John Wood, Fritsch, Verneau, Martin, and myself amounted to thirty-one, though it is possible that the same specimen may have been measured by more than one of these observers. The lowest brim index, 75·7, was that recorded by Fritsch, and the highest, 106, was the pelvis measured by John Wood; the mean of the series was 88·3. The measurements of the Negroes described by von Sömmerring, Vrolik, John Wood, Huxley, Barnard Davis, Spengel, Verneau, and myself amounted to thirty-five, though with them it is also possible that the same pelvis may have had its measurements recorded by more than one observer. The lowest brim index, 72, was measured by Spengel, and the highest a male described by John Wood, with an index of 105, whilst the mean of the series was 92·7. In the male Negro, therefore, there is a greater difference as a rule between the transverse and conjugate diameters than in the Australians, Bushmen, and Kaffirs, and the transverse diameter is proportionately wider. The males were mesatipellic, the females in the higher term of the platypellic division. The brim, therefore, as a rule, was not cuneiform, but had a more rounded outline.

The most extensive series of measurements of the pelvis in the Andaman Islanders has been given by Professor Flower in his memoir on their Osteology and in his Additional Observa-

tions thereon.¹ His measurements of the pelvic brim gave a mean index in thirteen females of 96.4 and in twelve males of 98.8. Dr Garson's measurements of apparently the same thirteen female pelvises furnish the same mean index 96.4. These numbers are higher than I got in my much more limited series (Table IV.), where the three adult females had a mean brim index of 87 and the single adult male an index of 97. Notwithstanding these differences, it is, however, quite clear that, as the brim index was about 98 in the males, the pelvis in this sex was distinctly in the dolichopellic division. In the females, again, the index was lower, and if the mean of Flower's and my observations be taken, it was 91.7, which places their pelvis in the mesatipellic group.

The measurements of a single male Nikobar Islander in the Berlin Museum have been given by Gustaf Fritsch in his Table II. The transverse diameter of the brim was 102 mm., the conjugate 91 mm., and the pelvic index was 89. It was therefore in the higher term of the platypellic division, but in all probability the mean index in this race will be found to be higher when a large average has been obtained.

Dr Barnard Davis has given the dimensions of the pelvis in three males and one female Tasmanian skeleton. The brim index in the female was 83, and the mean index of the three males was 93.3. M. Verneau has recorded the measurements of a single male Tasmanian pelvis; its transverse diameter was 108 mm., its conjugate 95 mm., and its brim index 88. The mean of the four male pelvises was 92, and not one exceeded 95, so that in all probability the Tasmanian pelvis is mesatipellic.

Amongst the Pacific Islanders M. Verneau has measured a fine series of pelvises from New Caledonia, three of which were females and twelve males. The mean transverse diameter of the brim in three females was 123 mm., the mean conjugate 110 mm., and the brim index was 89. The mean transverse diameter in twelve males was 114, the mean conjugate 104 mm. and the brim index was 91. The same observer has recorded the transverse diameter of the brim in a male Loyalty Islander from Lifu at 116 mm. and the conjugate diameter at 124 mm.,

¹ *Jour. of Anthropol. Inst.*, Nov. 1879 and Nov. 1884.

with a brim index 107; he has also given the transverse diameter of the brim in a male from New Guinea at 136 mm. and the conjugate at 113 mm., with a brim index of 83. His two male Sandwich Islanders had a mean transverse diameter of the brim of 114 mm. and a mean conjugate of 92 mm., which yielded a brim index of 81, and the mean brim index in my three female Sandwich Islanders was 83 (Table II.). M. Verneau's male pelvis from Tonga had a transverse diameter of 126 mm. and a conjugate of 121 mm., with a brim index of 96; his male pelvis from Mangareva had a transverse diameter of 119 mm. and a conjugate of 118 mm., with a brim index of 99; his male pelvis from Noukahiva had a transverse diameter of 108 mm. and a conjugate of 94 mm., with a brim index of 89. In my two New Zealand pelvises the mean brim index was 96. Dr Barnard Davis has given the transverse diameter of the brim of a male dolichocephalic Loyalty Islander from Lifu as 114 mm., and the conjugate as 106 mm., with an index 92; also the transverse diameter of a male brachycephalic Tannese as 121 mm., and the conjugate as 110 mm., with an index 81. Von Franque has stated the brim measurements of a female Papuan, from Lazon in the Philippine group, to be transverse diameter 115 mm., conjugate 110 mm., the index being 95.6. (Query—Can this have been a Negrito?)

There is therefore a wide range of variation in the relative transverse and conjugate diameters of the brim in the pelvises of the Pacific Islanders, so that the index ranged, amongst the pelvises measured, from 81 in a male Tannese and in a male Sandwich Islander to 107 in a male Loyalty Islander. This is in all probability to be accounted for, in part at least, from the fact that the series consisted of pelvises, some of which were obtained from islands populated chiefly by the Melanesian race, others chiefly by the Polynesian or Mahori race, others again by a mixture of the two races.¹ The specimens which have been measured are too few and too indefinite as to the race to which they belonged to enable one to state with any certainty what is the characteristic

¹ For a *résumé* of the facts on which a statement of the distribution of the two great races of the Pacific is made, I may refer to the chapter on the Races of the Pacific Ocean in the First or Craniological Part of my Report on the Bones collected during the voyage of H.M.S. "Challenger," part xxix., 1884.

form of the pelvic brim in each of these two great races, or the modifications which may arise in its form when the two races are intermingled. If one, however, may regard the pelves from New Caledonia as derived from the Melanesian race inhabiting that group of islands, then it would seem as if in the females the mean brim index did not reach 90, so that they belonged to the platypellic group, whilst in the males the same index was at or about 91, so that they were mesatipellic. On the other hand, however, in one of the male Loyalty Islanders, also in all probability of the Melanesian stock, the pelvic index was, as just stated, as high as 107, and therefore very strongly dolichopellic. Again, if one may regard the male pelves from Tonga, Mongareva, Noukahiva, and New Zealand as from people of the Polynesian or Mahori race, then it would seem as if this race had a higher brim index than the Melanesians, and was either dolichopellic or approaching that group. On the other hand, it should be remembered that the brim index in Verneau's two male Sandwich Islanders, and in Barnard Davis's brachycephalic Tannese, was as low as 81, *i.e.*, platypellic.

Should the opinion which I have just expressed, that the male Melanesians are mesatipellic, be confirmed by a more extended series of observations, then they will correspond in the form and proportions of the pelvic brim with the Negros rather than with the Australians, Bushmen, Hottentots, Kaffirs, and Andamanese, all of whom are distinctly dolichopellic. We may, however, look for much additional light on this matter when the observations which I understand Dr Prochownick of Hamburg is making on the large series of pelves from the Pacific Islands in the Godeffroy Museum have been published.

In addition to the specimens of the pelves of the Guanche people, measured in my Table VI., M. Verneau has recorded the characters of a male and female pelvis. Of the female he says that the inlet was very sensibly elongated antero-posteriorly, but on the contrary its transverse diameter was slightly diminished. With the exception of the inlet it differed very little from a European woman. The transverse diameter of the brim was 132 mm., the conjugate 120 mm., and the brim index was 91. In his male as in the female the transverse diameter of the brim only exceeds the antero-posterior by a few milli-

metres, and the brim index was also 91. In my perfect male pelvis the transverse diameter considerably exceeded the antero-posterior, the brim index was 85 and the form of the inlet approximated to the oval. The mean of the two males was 88, but the specimens are too few to enable one to state definitely to which of my three divisions of the pelvis this race should be referred, but in all probability it is either platypellic or mesatipellic.

The dimensions of the brim in an Esquimaux pelvis have been recorded by Dr Struthers¹ in a female specimen. He gives the conjugate diameter as (4½ inches) 117 mm., and the transverse as (6 inches) 153 mm., which furnish a brim index of 76, and show a pelvis which must have had a markedly transversely oval inlet. M. Verneau records the transverse diameter of the brim in his male pelvis as 124 mm., but it was too much damaged to enable him to obtain the conjugate dimension. In my two specimens the brim index, 88 in the male and 84 in the female, closely corresponded to the mean index in Europeans of both sexes (Table VII.). It is probable that the Esquimaux therefore may belong to the platypellic group.

The two male Laplanders whose pelvic measurements are recorded by M. Verneau had a mean transverse diameter 122 mm. and a mean conjugate diameter 101, so that the brim index was 83. In my male specimen the transverse diameter was much smaller, both absolutely and relatively to the conjugate, and the brim index was 93. In my female, again, the transverse diameter of the brim was considerably in excess of the conjugate, and the pelvic index was only 72.5 (Table VII.). The mean brim index of the three males was 88, and it is not unlikely that the male Lapp pelvis may, when additional observations are recorded, be found to be in the higher term of the platypellic group.

The Mongolian race is represented in my measurements in Table V. by a single Chinese pelvis, which, from the label attached to it, I have described as a male, though in the open subpubic angle, 76°, it approximated to the female character. Apparently only four Chinese pelves had previously been described, a female by von Franque, a male and female by

¹ *Anatomical and Physiological Observations*, Edinburgh, 1854.

Verneau and a male by Spengel. Verneau, in addition, gives an account of a male Annamite. Von Franque pointed out¹ that it was scarcely possible to distinguish the pelvis of his Chinese woman from that of an European; the transverse diameter of the brim was 133 mm., the conjugate 104 mm., so that the brim index was 78. Verneau stated that the inlet in the Chinese woman was very enlarged, very prominent, and had the form of a heart on a playing card. The transverse diameter of the brim was 140 mm. and the conjugate 89 mm., so that the brim index was only 64, being the lowest pelvic index recorded in his series of measurements. In his male Chinese the transverse diameter was 115 mm., the conjugate 93 mm., and the brim index was 81. Spengel's male had a transverse diameter 112 mm., conjugate 95 mm., and the pelvic index was 85. In my specimen the corresponding index was 85, and it is not unlikely that the mean index of the Chinese, when a sufficient number have been measured, will ultimately prove to be platypellic. Verneau's Annamite male pelvis had an inlet 110 mm. in its transverse and 88 mm. in its antero-posterior diameter, with an index of 75, which strengthens the view that the Mongolian pelvis is platypellic.

Dönitz,² from the study of seven Japanese pelves, apparently females, has come to the conclusion that two different types were to be found in them, the one with a round or heart-shaped inlet, the other with a transversely oval or wide brim. Those with a round or heart-shaped inlet he regarded as belonging to the Malayan race, whilst those with a wide brim, approximating to the Europeans, he held, according to an hypothesis of Wernich, to be a product of a cross between the Aïnos, the original inhabitants, and the Malays. Scheube³ has measured a male Aïno pelvis, and has given the transverse diameter of the brim as 113 mm. and the conjugate as 115 mm., which give a brim index 102. Barnard Davis's measurements⁴ of the pelvis of an Aïno woman are transverse diameter 102 mm., conjugate 117, with a pelvic index 97. In each pelvis,

¹ Scanzoni's *Beiträge zur Geburtskunde*, vol. vi., Würzburg, 1869.

² Quoted by Ploss in *Archiv f. Anthropologie*, Bd. xv. p. 566, 1884.

³ Also quoted by Ploss.

⁴ Supplement to *Thesaurus Craniorum*, Table II.

male and female, the brim index was above 95, so that it is possible that the Aïnos are dolichopellic.

If these measurements of the Aïno pelvis are to be regarded as expressing the character of the race, it is difficult to see how a people with such dolichopellic proportions, by crossing with a race in which the conjugate diameter is also proportionately great, could produce a pelvis with a wide inlet.

The male Malayan pelvis measured in my Table V. had an inlet which was ovoid in the antero-posterior diameter, and the brim index, 105, showed it to be highly dolichopellic. The two male Javan pelves measured by Barnard Davis are, however, stated to have had a pelvic index 83 and 81 respectively, *i.e.*, they were platypellic. In a female Javan pelvis measured by Verneau this index was 90. In a female measured by von Franque, it was 92. Zaaïjer, from his analysis of the pelvic measurements of twenty-six women, stated that the form of the inlet was not uniform; in sixteen it was round, the transverse diameter being to the conjugate as 100 to 90 or under, in ten it was longish-oval, the transverse diameter being as 100 to more than 90. H. Fritsch has measured five Malay pelves, and has described the pelvic inlet as round with a relative predominance of the conjugate diameter. C. Martin has described the conjugate diameter as very long, the inlet round, in many examples oval. From the series of female Malay pelves described by Zaaïjer, H. Fritsch, and himself, C. Martin has obtained a mean transverse diameter of 119 mm. and a mean conjugate of 109 mm., from which a brim index of 91.6 can be computed, so that they are mesatipellic. This is a high index for the female sex, and as experience has shown that in each race the brim index is, as a rule, distinctly higher in the male than in the female, it is not unlikely that the male pelves are dolichopellic, and the high index in my male specimen is probably a key to the dolichopellic character of these people.

I have had no opportunity of examining any pelves of the Indian tribes of either North or South America. Very little, indeed, appears to be known of the pelvis in the North American Indians. Von Franque has described a male and a female pelvis of Flat-head Indians, and from his measurements the

brim index in the male was 76 and in the female 84.5. Barnard Davis, in his *Thesaurus Craniorum*, table, p. 367, states that the pelvic index in a male Illinois Indian is 86. The mean of these two male North American Indian pelves is 81.

Weber, Barnard Davis, and Verneau have all described specimens of the pelvis in various tribes of South American Indians. Weber figures the pelvis of a male Botocudo Indian, the diameters of the brim in which give the index 85; also a female Botocudon, the brim diameters of which give an index 107. He places the male in his group of pelves with an oval inlet, the female in his cuneiform group. Barnard Davis found the conjugate and transverse diameters of the brim in a male Puelche Indian to be equal at 116 mm., with an index therefore of 100, but in the pelvis of an ancient male Peruvian the index was only 81. Verneau gives the transverse diameter of the brim in a male Charruan Indian as 122 mm. and the conjugate as 115 mm., the index being 94; also the transverse diameter of a male Botocudon as 123 mm. and the conjugate as 91 mm., the index being 74; also the transverse diameter of a male Goytacazen 119 mm. and the conjugate 89 mm., with an index 75, and of a female with an index 86; also the mean transverse diameter of two male Peruvians 135 mm. and the conjugate 91 mm., with a mean index 67, and three females with a mean index 83; also a male Bolivian with a transverse diameter 116 mm. and a conjugate 105 mm., the index being 90.5; also a female Mexican¹ with a transverse diameter 130 mm. and a conjugate 104 mm., the brim index being 80. The males measured by Verneau varied in the brim index from 67 in the Peruvians to 94 in the Charruan, with a mean on the six specimens of 80; the females were much more uniform in the brim index, with a mean on the five specimens of 83. The American Indians presented this peculiarity that the mean pelvic index in the female was higher than in the male, and that therefore the transverse diameter was not proportionally so much in excess of the conjugate. The mean brim index computed from the whole series of measurements above of the pelvis of South American Indians is 83.3 for the males, and 89 for the females, so that if this

¹ Although he refers to a male Mexican pelvis in the Museum, yet he does not give its measurements.

average should be confirmed by a larger series of measurements, the pelvis in these people is platypellic. Carl Martin, from his own observations and those of von Franque, has given the mean transverse diameter of the brim in both North and South American aboriginal women at 127 mm. and the mean conjugate at 115, from which an index of 90.5 can be computed, which is somewhat higher than the mean obtained from the pelves above enumerated.

I shall now classify in three parallel columns the people or races whose pelvic brim index I have analysed, both from my own observations and from those of other anatomists, in the preceding pages. For reasons to which I have already referred, I have not included the female pelvis in this classification, and have based it entirely on the measurements of the male pelvis; though, as will be seen from the frequent references which I have made to the brim index in the female, I consider that it assists one in arriving at a conclusion as to the group in which the pelvis of each race should be placed. In those cases in which, from the few pelves which have been measured, there may be a doubt as to the group in which a people or race should be placed I have appended a query.

<i>Dolichopellic.</i>	<i>Mesatipellic.</i>	<i>Platypellic.</i>
Australians	Negroes	British
Bushmen	Tasmanians	French
Hottentots	New Caledonians	Germans
Kaffirs	Melanesians generally ?	Europeans generally
Andamans	...	Guanche ?
New Zealanders ?	...	Esquimaux ?
Polynesians generally ?	...	Laplanners ?
Malays	...	Chinese
Ainos ?	...	Mongolians generally
		American Indians

How greatly the female pelvis is modified in the proportions of the pelvic brim, in relation to the special sexual requirements, is shown from the fact that in none of the people or races whose pelvic dimensions are analysed in sufficient numbers to enable one to obtain an average, does the female pelvis attain in the mean of each race dolichopellic proportions. Thus, in the Australians, Andaman Islanders, and probably the Malays,

whilst the males are dolichopellic the females are mesatipellic. In the Bush race the males are dolichopellic, the females platypellic. In the Kaffirs the males are dolichopellic, the females mesatipellic or platypellic. In the Negroes and New Caledonians the males are mesatipellic, the females are platypellic. Amongst the Europeans generally with a platypellic male index the females are still more platypellic. In the South American Indians, however, whilst the males are platypellic, the females are on the verge of being mesatipellic. These modifications all signify that in each race or people the transverse diameter both of the brim, the cavity, and the outlet are as a rule relatively, and indeed for the most part absolutely, wider in the female pelvis than in the male.

In the Tables of measurements of the pelvis in various races of men, to which I have already referred as forming a part of my Report on the Bones of the Skeleton collected by H.M.S. "Challenger," I have given the maximum length and breadth of the sacrum, and have computed a sacral index, multiplying the breadth by 100 and dividing by the length. When the sacral index is above 100, the breadth of the bone is of course greater than the length, when below 100 the length exceeds the breadth. From my own measurements and those of other observers I have obtained the mean sacral index in the male pelvis, as in the following table :—

	Sacral Index.		Sacral Index.
Australians	98	Negroes	105·5
Bush	94	Europeans	112
Kaffirs	92·8		
Andamanese	94		

It will be seen, therefore, that in the Australians, Bush, Kaffirs, and Andamanese the sacrum is longer than broad. In the Europeans the breadth materially exceeds the length, whilst in the Negroes, though the mean breadth exceeds the length, it does not do so to the same extent as in the Europeans. Both in the dolichopellic proportions of the pelvic brim and in the greater length of the sacrum than in its breadth, the Australians, Bush, Kaffirs, and Andamanese present a closer approximation to the relative proportions of the parts found in the pelves of

apes, and those other mammals that possess five vertebræ in the sacrum, than is the case in the Negroes and in the Europeans. The pelvis, therefore, in those races shows a more degraded character—a less departure from the usual mammalian form—than is the case in the Europeans. In the Negro, again, the pelvis, both in the relations of its pelvic brim and in the proportions of its sacrum, approximates more closely to the European than to other black-skinned races.

THE ANATOMY OF A SECOND SPECIMEN OF
SOWERBY'S WHALE (*Mesoplodon bidens*) FROM
SHETLAND. By Professor W. TURNER, M.B., LL.D.,
F.R.S. (PLATE IV.)¹

THE Shetland seas are frequented by several species of Ziphioid whales. Since the year 1870, I have come into possession of, and placed in the Anatomical Museum of the University of Edinburgh, the skull of *Ziphius cavirostris*,² the skull and a large part of the skeleton of *Hyperoodon rostratus*, and the skull and almost complete skeleton of *Mesoplodon bidens*.³ They were all captured on the north-east side of the mainland of Shetland.

On the 2nd June of this year, Mr Charles Anderson, one of my students, told me that a small whale had been taken a few days previously at Voxter Voe, Delting, and he has kindly furnished me with the following account of its capture:—On the 23rd May it was seen in Sullom Voe, and on the 25th it was heard by two fishermen blowing in Voxter Voe, a small creek on the south side of Sullom Voe. They started in a small boat in pursuit of the whale, and by shouting and throwing stones they drove it to the head of the Voe, where it stranded. A young one, about 7 feet long, was seen with it, which escaped by diving below the boat. The men then attacked the stranded animal both with a clasp knife and a "toiskar" (a sort of spade used in Shetland for cutting peats), and with the latter instrument cut one of the large arteries, from which a jet of blood spouted for several minutes. As the animal was struggling dangerously the tail was then cut off, and it died immediately afterwards.

Voxter Voe is about thirteen miles from Urafirth Voe, where in April 1881 the first specimen of *Mesoplodon bidens* above referred to had been captured by his brother, Mr Thomas

¹ The substance of this article was communicated at Aberdeen to the British Association for the Advancement of Science, September 11, 1885.

² Described and figured in *Trans. Roy. Soc. Edin.*, May 20, 1872, vol. xxvi.

³ Described to the Royal Society of Edinburgh, Jan. 30, 1882. See *Proceedings* of that date, also *Journal of Anatomy and Physiology*, April 1882.

Anderson of Hillewick. Mr Charles Anderson informed me that, from the description which his brother had written to him of the Voxter Voe specimen, it was also, he believed, a Sowerby's whale. I telegraphed therefore to Mr Thomas Inkster of Brae, near Voxter Voe, to secure the animal for me as little injured as possible. On the 15th of June it arrived at the University, and proved to be a fine specimen of an adult male *Mesoplodon bidens*. From this specimen I hope to complete the description of the skeleton of this animal, which, owing to several bones being missing in the 1881 specimen, was necessarily incomplete, and to supply also some information on the anatomy of the soft parts, about which little, if anything, is known.

EXTERNAL CHARACTERS.

From Mr Charles Anderson's notes I am able to state that this specimen, like the one captured in 1881, was dark slate-coloured on the back. The belly was dirty white, and with a ribbed appearance extending backwards from the jaw for about two-thirds the length of the animal. It had also a crevice between the two halves of the lower jaw. The two large mandibular teeth, projected like tusks from the sides of the mouth. The whale had been flensed, eviscerated, and cut into blocks before being despatched to me. All the skin had been removed except that of the tail and flippers. The thoracic and abdominal viscera had been removed *en masse*, and accompanied the divided carcass. From the extent to which the animal had been cut up, my notes on the soft parts are necessarily very fragmentary, and as the specimen reached me in the hot weather in June, more than a fortnight after the death of the whale, the viscera could not be examined with that minuteness which I should have desired.

I placed the various blocks together in their proper positions, and ascertained that the length, from the tip of the lower jaw to the mid-point on the posterior edge of the tail, was 15 feet 8 inches. The width of the tail between its tips in a straight line was 3 feet 10 inches; the antero-posterior diameter of the middle of the tail was 1 foot 2 inches. The skin of the tail was shining dark slate-grey, almost black, both on the dorsal and the ventral surface; it had a mesial keel extending for a short

distance from before backwards both on its dorsal and ventral surfaces. The anterior border of each wing of the tail was convex; the posterior border of the entire tail was concave from tip to tip, but it swelled out slightly in the middle of this border so as to have a festooned edge, and without any notch at the middle of the tail. The flipper was 1 foot 10 inches from the head of the humerus to the end of the flipper, and its greatest antero-posterior diameter was $6\frac{1}{4}$ inches. Its colour on both surfaces was like that of a well-blackened boot. It came almost to a point at the tip, the anterior border was slightly convex, the posterior border for 7 inches from the axilla was almost straight and then rapidly sloped forward to the tip. Both the tail and flipper corresponded closely in shape to those of the Ziphioid figured by Burmeister as *Epiodon patachonicum* or *australe*,¹ but which is probably the same species as *Ziphius cavirostris*.²

MOUTH, THORACIC AND ABDOMINAL VISCERA.

The pair of mandibular teeth projected for one inch beyond the gum. On separating the jaws the tip of the tongue was seen to lie midway between the pair of mandibular teeth. A semicircular projection, with the concavity directed backwards, of the mucous membrane of the floor of the mouth was opposite the tip of the tongue; from this projection to the free end of the mandible the mucous membrane was smooth, concave from side to side, and continuous with the gum which covered the edge of the mandible. The mucous membrane behind this semicircle was raised into ridges running from before backwards, and continuous with it was a broad fold, which passed to the under surface of the anterior part of the tongue, and formed a strong frænum. The dorsum of the tongue was studded with crypt-like depressions and papillæ, amongst which a V-shaped arrangement of circumvallate papillæ was seen. The tip of the tongue was movable both from side to side and from before backwards. The mucous membrane of the palate was pitted with numerous small depressions. The

¹ *Anales de Museo Publico de Buenos Aires*, Entrega quinta, tom. i., plate xv.

² See my account of *Ziphius cavirostris* in *Trans. Roy. Soc. Edinburgh*, 1872, and also *Challenger Reports*, part iv. vol. i., 1880.

hand could easily be passed backwards through the fauces into the pharynx, and could be made to grasp the elongated upper end of the larynx, which fitted into the posterior nares, not so closely, however, as to prevent the finger from being at the same time introduced into the nares. The blowhole was transverse and not as in the former specimen semilunar, and its long diameter was $3\frac{1}{2}$ inches. On the surface of the head it was not divided into two nostrils, but further into the nose this division was effected by the mes-ethmoid. Opposite the entrance into each division of the nose the mucous membrane formed a definite raised area, corresponding in size and shape to each opening; and bounding each area above was a strong fold of the membrane, which formed, apparently in connection with the corresponding raised area, a valve-like arrangement for the opening.

Œsophagus and Stomach.—The œsophagus opened behind into the elongated 1st compartment of the stomach by a patent orifice without a valve-like sphincter. The œsophageal mucous membrane was elevated into fine crenulated ridges having a longitudinal direction, which ended at the opening into the 1st or proximal compartment in a sharp but somewhat irregular fold of mucous membrane, which surrounded the opening into the stomach. It was strongly differentiated from the mucous lining of this compartment, not only by this fold, but by the size and direction of its mucous ridges and by its yellowish colour. The 1st compartment was 19 inches long and 9 inches wide in its greatest transverse diameter. Its muscular wall was very strong and quite half an inch thick at its hinder end, though nearer the œsophagus it was thinner; from differences in colour, the muscular coat obviously consisted of two layers. Its mucous lining was of an opaque whitish tint, and elevated into broad and highly convoluted folds separated by narrow furrows. Continuous with, and set at an angle to, its hinder end, was the 2nd compartment of the stomach, which opened into the 1st compartment a little in front of that end which was furthest away from the œsophagus. This opening admitted three fingers, and was surrounded by a valve-like fold of the mucous membrane. Beyond the 1st compartment the outer surface of the stomach was marked by a series of constrictions, which pointed

to a subdivision of the organ into several compartments, which were successively opened into.

The 2nd compartment was globular in shape, and was no larger than a moderate sized orange, and its mucous membrane was smooth. On the wall opposite to the aperture into the 1st compartment the orifice of communication with the 3rd compartment was situated, which was bounded by a raised valve-like fold of mucous membrane. The 3rd compartment was about three times bigger than the second, and its

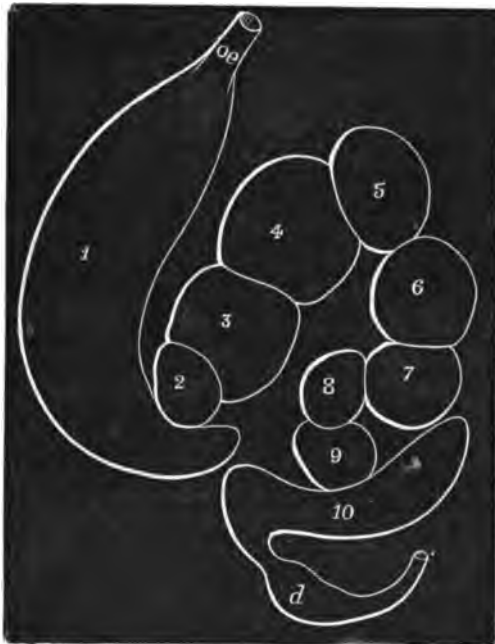


FIG A.—Diagram to illustrate the compartments of the stomach of Sowerby's whale (*Mesoplodon bidens*).

mucous lining was rugose. It communicated with the 4th compartment by a similar opening in the wall opposite to that by which it communicated with the 2nd compartment. The 4th compartment was about equal in size to the 3rd. Its mucous lining was in part smooth, but projecting from one part of the wall was a rugose convoluted area of mucous membrane, which, though attached by a broad peduncle, could be freely moved about in the cavity. This area probably contained a large collection of gastric glands. The 4th communicated with the 5th compart-

ment by an orifice which had a double fold of mucous membrane surrounding it, and between the two divisions of this fold was a pouch large enough to hold a small walnut. The 5th compartment was somewhat smaller than the 4th. Its mucous lining was smooth, except on one convoluted area. It communicated with the 6th compartment by an orifice surrounded by a valvular fold, which was situated close to the aperture of communication of the 5th and 4th compartments with each other and not in the opposite wall. The 6th compartment was of about the same size, and possessed a similar mucous lining to the 5th compartment. It communicated with the 7th compartment by an opening like that between the 5th and 6th. The 7th compartment was like the 6th in size, and had a similar mucosa. It communicated with the 8th compartment by an opening close to that between 6 and 7, but this opening barely admitted two fingers. The several cavities from 1 to 7, both inclusive, contained a brownish mucus, but no other contents. The 8th compartment was about as big as a good sized orange and had a convoluted mucous lining. It contained a bile-stained fluid with a number of opaque crystalline lenses and elongated calcareous bodies about $\frac{1}{4}$ inch long, the nature of which it was difficult to state, but which might be the otoliths of fish. Its communication with the 9th compartment was almost opposite the opening into 7. The 9th compartment was of the same size as 8. It had also similar contents, and possessed a raised patch of convoluted mucous membrane. Its communication with the 10th compartment only admitted two fingers, and had the usual mucous fold around it. The compartments from 2 to 9, both inclusive, formed an intercommunicating series of globular cavities closely resembling each other in general appearance and presenting no great difference in size. Their muscular walls, as well as that of 10, were not so thick as the muscular wall of the first compartment.

The 10th or distal compartment differed from the last named very materially both in size and shape. It was indeed not unlike a large human stomach in its outward form. Internally, however, it had projecting into its cavity a strong crescentic fold of the mucous membrane, which mapped it out into two almost equal subdivisions, with one of which the 9th compartment communi-

cated by an opening close to one horn of the crescentic fold. The wall of this subdivision was in close relation to the wall of 9, and the cavity formed at one end a large cul-de-sac. The other subdivision communicated with the duodenum, the opening into which was situated near the other horn of the crescentic fold; this opening barely admitted two fingers and was surrounded by a pyloric valve. The 10th compartment contained several ounces of a bile-stained fluid, and its mucous lining was thick and rugose.

Intestine.—The duodenum formed at its junction with the stomach a cylindriciform passage $1\frac{1}{2}$ inch long and 1 inch wide, which dilated into a funnel-shaped tube, and soon became again cylindriciform. Its mucous lining was bile-stained and was elevated into valvulæ conniventes, which had a reticulated arrangement and contained many small pockets in the meshes. In close relation to the outer wall both of the duodenum and last compartment of the stomach was situated the *Pancreas*, the duct of which was exposed by dissecting away the gland substance. This duct was about as large as the human femoral artery, and extended for a short distance in contact with the wall of the duodenum, which it then pierced very obliquely and opened into the funnel-shaped part of that intestine about five inches from the pylorus. The opening was not on a papilla but on the plane surface, in the interval between reticulated valvulæ conniventes. The bile duct, though looked for in relation to the wall of the duodenum, was not detected; it had possibly joined the pancreatic duct in the substance of the pancreas—as I found to be the arrangement in a *Globiocephalus melas* which I dissected in 1867¹—at a point nearer the liver than where the pancreatic duct was exposed. About 60 feet of intestine were measured, but they did not represent the whole length of this canal.

The *Liver* was a large organ divided into two lobes by a falciform ligament. The hepatic veins joined the inferior vena cava where it pierced the diaphragm. Broad valve-like folds of the lining membrane projected into the vena cava.

All anatomists agree that the stomach in the Cetacea is compound as regards the number of its compartments. It is in the

¹ See *Jour. Anat. and Phys.*, Nov. 1867, vol. ii.

Ziphioid group of whales that these compartments attain their maximum number. In Hyperoodon, the best known of the Ziphioids, John Hunter found¹ that the stomach consisted of seven compartments, and that an eighth dilatation was present, which, as the bile ducts entered it, he regarded as duodenal and not gastric. Dr A. Jacob described and figured² the dried and inflated stomach of a Hyperoodon which he had dissected.

The first compartment is an oval cavity 2 feet 6 inches long and 12 inches in diameter. This is followed by seven spherical cavities³ more or less flattened at the sides where they come in contact with each other, and they increase successively in size until the seventh and eighth. He also says that the duodenum is about 6 inches in diameter, but tapers gradually, within a distance of 12 inches, to the diameter of the intestine. He is not clear whether it is to this dilatation that John Hunter referred when speaking of the bile ducts entering it. Dr Jacob was quite sure that in his specimen eight distinct cavities were present before this enlargement of the duodenum.

Vrolik, in his important monograph "van den Hyperoodon,"⁴ has described and figured the stomach, the characters of which he summarises as follows:—

The stomach consists of a cardiac and a pyloric end. The cardiac end forms one cavity and is lined by mucous membrane in longitudinal folds, which under the microscope consists of a reticular network of small microscopic cavities. The pyloric end is divided into six compartments lined by smooth mucous membrane, but which under the microscope seems to consist of mucous glands closely packed together. These compartments increase in transverse diameter from the cardiac to the duodenal end of the stomach, and are continuous with each other through intermediate openings, which openings are directed towards the lesser curvature of the stomach; the sixth of these compartments forms a *cul-de-sac* at the pyloric end, and from this sac leads the opening into the duodenum, which is 0·40 EL. wide at its commencement and diminishes to 0·20 EL. in width.

¹ *Structure and Economy of Whales*, vol. iv. pp. 359, 360, of Palmer's edition of his collected works.

² "On the Generic Characters and Anatomical Structure of the Whale entitled *Delphinus diodon*," by Hunter, and "*Hyperoodon*," by Lacepède, in *Dublin Philosophical Journal and Scientific Review*, vol. i. p. 58, 1825, reprinted in *Essays, Anatomical, Zoological, &c.*, Dublin, 1845. This excellent account of Hyperoodon has been far too much overlooked by subsequent writers.

³ In the text he says "eight spherical cells or cavities," but this obviously should read seven, as there are only seven spherical cavities represented in his figure, in addition to the elongated oval cavity directly continuous with the cesophagus, which is the first compartment, making thus in all eight cavities.

⁴ Haarlem, 1848.—I am indebted to my pupil Mr E. B. Glaeser for a translation from the Dutch of Vrolik's description.

In the following year Eschricht described¹ the stomach of a specimen of *Hyperoodon* dissected in 1841.

He states that the first compartment, 6 inches long and 3 inches in width, is a sac-like dilatation of the hinder end of the œsophagus, and that it is lined by the thick epithelium of that tube, which suddenly ends at the opening into the 2nd compartment, which is not unlike in shape to the human stomach, and is 1 foot·8 inches long in a straight line. Its inner wall is soft, strongly corrugated (*gerunzelt*), and reddish-coloured, and very like the second stomach of Cetacea generally. Then follows, what, on an external view, seems to be a large compartment, 2 feet long and 10 inches in greatest width, but when opened into it is seen to consist of seven compartments, separated from each other by six circular valves; the inner surface of these cavities is smooth, soft, whitish, and without marked folds of mucous membrane. Thus Eschricht saw as many as nine compartments in his specimen.

In the Anatomical Museum of the University of Edinburgh is an inflated and dried specimen of the stomach of *Hyperoodon rostratus*.

It possesses seven definite compartments. The 1st compartment is 17 inches long and 9 inches in its widest part, and in its elongated shape resembles somewhat the human stomach, though it does not possess so great a dilatation at its œsophageal end. It freely communicates by a large orifice with the œsophagus; close to its opposite end it is continuous with the 2nd compartment, which is globular in shape and about the size of a very large orange. The 2nd compartment communicates with the 3rd, the 3rd with the 4th, the 4th with the 5th, and the 5th with the 6th. Compartments 3 to 6 inclusive are all somewhat globular in form, and of almost equal magnitude, being about three times the size of the 2nd compartment. The 6th compartment opens into the 7th, which is 12 inches long in its transverse diameter and $8\frac{1}{2}$ inches in its vertical. This will probably correspond with the last compartment of the stomach, as described by Vrolik, but it is succeeded by an elongated and somewhat kidney-shaped sac $8\frac{1}{2}$ inches long by $4\frac{1}{2}$ inches at its widest part. This sac is separated from the 7th compartment by a circular flattened band of mucous membrane perforated in the centre by a small opening, and it projects beyond this opening for 4 inches as a rounded *cul-de-sac*. It communicates at its narrowest end with the cylindriciform intestine by a constricted opening. In the absence of the biliary and pancreatic ducts it is not possible to pronounce definitely if this sac is a compartment of the stomach or a mere dilatation of the beginning of the duodenum.

Burmeister has described² the stomach in the Ziphioid whale

¹ *Untersuch. über die Nordischen Wallthiere*, p. 40, 1849.

² *Anales del Museo publico de Buenos Aires*, vol. i. p. 356.

which he has named *Epiodon patachonichum* or *australe*, but which is probably *Ziphius cavirostris*.

The stomach consists of eight compartments. The 1st compartment is shaped like a pear, and divided by a constriction into two unequal parts, of which the anterior has more than double the bulk of the posterior. The 2nd and 3rd compartments are almost of equal bulk, but very much smaller than the 1st, and each consists of an oval sac. The 4th and 5th compartments are more united with each other than the others are, and their bulk is considerably less than that of the 1st. The 6th and 7th compartments are again very small, and similar to the 2nd and 3rd in form and size. The 8th compartment is the largest, and kidney-shaped. The aperture by which it opens into the 7th compartment is in the middle of its concave border, and the pyloric outlet into the duodenum is immediately below the opening into the 7th. The duodenum commences, not by a dilatation, but by a constriction extending at first insensibly, and continuing afterwards as the cylindrical tube of the small intestine. Immediately after its commencement the duodenum receives two ducts, the hepatic and the pancreatic, which enter the duodenum at a short distance from each other.

It will now be of much interest to compare the stomach of the Ziphioid whales with the same organ in other Cetacea, and as the stomach in the Delphinidæ has been most frequently and carefully examined, I shall begin with that group, and in the first instance speak of the number of compartments. In the Common Porpoise (*Phocæna communis*) Edward Tyson¹ stated that the stomach consisted of three bags, and of a long descending passage which connected the 2nd and 3rd compartments with each other. Sir Richard Owen,² Dr J. B. S. Jackson,³ Dr Knox,⁴ and myself⁵ have each described four gastric compartments in this animal, the long descending passage of Tyson being regarded as a compartment of the stomach. John Hunter⁶ and Dr Jacob⁷ each speak of five compartments, but their 5th is without doubt the dilated commencement of the duodenum.

¹ *Phocæna, or the Anatomy of a Porpoise*, London, 1680.

² Note to Palmer's edition of Hunter's Works, vol. iv. p. 360, and *Comp. Anat. of Vertebrates*, vol. iii.

³ *Boston Journal of Natural History*, vol. v. p. 167, 1845.

⁴ *Proc. Linnean Soc.*, 1857.

⁵ *Journal of Anat. and Phys.*, vol. ii. p. 70, Nov. 1867, and vol. iii., Nov. 1868.

⁶ Palmer's Edition of Hunter's Works, vol. iv. p. 359.

⁷ *Op. cit.*

In *Delphinus albirostris* (*Lagenorhynchus*) both Mr J. W. Clark¹ and Professor Cleland² have each recognised four compartments. In *Orcella brevirostris* Dr John Anderson has described³ three cavities, and "an intervening narrow funnel-shaped channel between the second and third sacs." This channel is probably the same as what I have called the third stomach of the Porpoise, so that on this view *Orcella* would also have four compartments. In *Globiocephalus melas*, both Dr Jackson and I have described five compartments, though Dr Murie⁴ regards the compartment, which

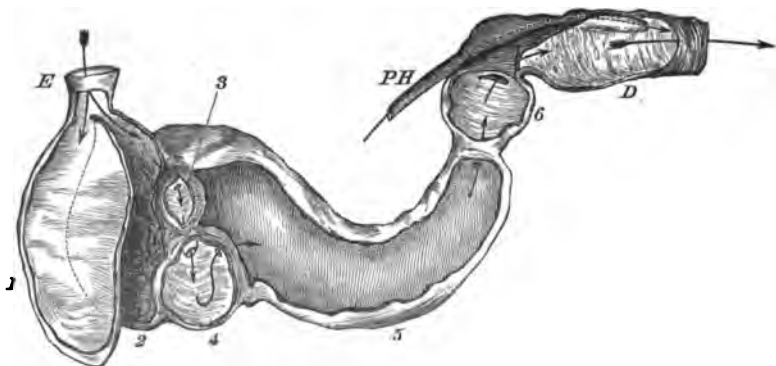


FIG. B.—Stomach of young Pilot-Whale (*Globiocephalus melas*). E, Esophagus; 1 to 5 inclusive, the five compartments of the stomach; 6, the dilatation immediately preceding the cylindrical duodenum D; PH, the conjoined pancreatic hepatic duct.

I have numbered 3, not as a true digestive sac, but only as a communicating canal. With this interpretation, however, I am unable to agree, and still adhere to my opinion that it is a true though small gastric compartment. As I shall frequently have to refer in the course of this comparison to the stomach of *Globiocephalus*, I reproduce here, for convenience of reference, my original figure of the organ in that animal. From Cuvier's description⁵ of the stomach of *Delphinus delphis*, it would seem as if it also possessed five divisions. In the Grampus (*Orca gladiator*) John Hunter found five compartments. In

¹ *Proc. Zool. Soc. London*, June 20, 1876.

² *Journal of Anat. and Phys.*, vol. xviii., 1884.

³ *Anatomical and Zoological Researches*, p. 374, 1878.

⁴ *Trans. Zool. Soc. London*, vol. viii.

⁵ *Leçons d'Anatomie Comparée*, vol. iv. p. 79, 1835.

Grampus rissoanus Dr Murie stated that the stomach closely corresponded with that of *Globiocephalus*; and from M. Fischer's description¹ a similar arrangement was possessed by *Grampus griseus*. In the White Whale (*Delphinapterus leucas*) Professor Wyman² recognised five gastric compartments, and the same number have been described by Drs Watson and Young in their specimen.³ One may also infer from the short reference made by Meckel to the stomach of the Narwhal (*Monodon monoceros*) that it also had five compartments.⁴

In the *Delphinidæ*, the first, œsophageal, or proximal compartment is continuous with the œsophagus, and, as was recognised by Edward Tyson two hundred years ago in the Porpoise, is lined by a continuation of its inward tunic, which we now know to be squamous epithelium, so that it seems to be a sac-like dilatation of that tube or a paunch; whilst the distal or pyloric compartment, which lies in relation to the duodenum, is elongated in form, and, with its mucous membrane, is usually bile-stained. Between the paunch-like proximal and the elongated distal compartments are either two or three more or less globular compartments, which, like the distal compartment, are without doubt active agents in the digestive process.

At the first glance it might seem as if in Sowerby's Whale, and in the other Ziphioids in which the stomach has been described, the general plan of construction resembled that met with in the *Delphinidæ*, viz., a proximal paunch, a distal or pyloric compartment, and an intermediate series of globular compartments, which are more numerous, however, in the Ziphioids than in the Dolphins, and attain their maximum number in Sowerby's Whale. But a more careful comparative study of the stomach in these families of Cetacea has satisfied me that much more important morphological differences exist between them. What these differences are I shall now explain, and the point to which I shall first direct attention is the relation of the gastric orifice of the œsophagus to the 1st and 2nd compartments of the stomach.

¹ *Annales des Sciences Naturelles*, viii. p. 363, 1867.

² *Boston Journal of Nat. Hist.*, vol. vii.

³ *Trans. Roy. Soc. Edinburgh*, vol. xxix., 1879.

⁴ *System der vergleich. Anatomie*, vol. iv. p. 527, 1829.

In *Globiocephalus melas*, as I pointed out some years ago, the œsophagus communicates freely with the 1st and 2nd compartments, and a similar arrangement exists in *Grampus rissoanus* (Murie), *G. griseus* (Fischer) and *Lagenorhynchus albirostris* (Clark and Cleland). In the *Phocæna communis*, the 2nd compartment opens out of the 1st in close proximity to the œsophagus, and a similar arrangement has been seen in *Delphinapterus leucas* (Watson and Young). In *Mesoplodon bidens*, on the other hand, the 2nd compartment opens out of the 1st in proximity to the end furthest away from the œsophagus, and a similar arrangement was found by Jacob, Vrolik, and myself in *Hyperoodon*. In Burmeister's Ziphioid it is also clear, from his description, that whilst the œsophagus opens into the anterior wall of the 1st compartment in front of the constriction, the communication with the 2nd compartment is behind the constriction. In all these Ziphioids, therefore, the 2nd compartment opened out of the 1st at a considerable distance from the œsophagus, which interval, both in *Mesoplodon* and *Hyperoodon*, was equal almost to the length of the 1st compartment.

But further, whilst examining the stomach of Sowerby's Whale I was particularly struck with the difference in colour between the œsophageal mucous membrane and that of the 1st gastric compartment; also with the contrast between the fine longitudinal folds of the mucous lining of the œsophagus and the broad convoluted folds of the mucous lining of that compartment, and with the elevated irregular fold of mucous membrane which differentiated the œsophagus from the stomach. I felt therefore that important structural differences would, without doubt, exist between the œsophageal mucous membrane and that of the 1st gastric compartment. This was at once confirmed on making a microscopic examination of the epithelial covering, which in the œsophagus could be separated in distinct flakes composed of squamous cells; whilst in the stomach the epithelium did not peel off in flakes visible to the naked eye, but was much more delicate and more easily disintegrated, and consisted of columnar cells with granular contents, lying amidst debris, formed apparently of broken-down epithelium. As I felt it necessary, however, to make a more complete examination of the two mucous

membranes I requested my museum assistant, Mr James Simpson, to prepare vertical sections, and notwithstanding the unfavourable conditions, as regards time after death, under which the examination was made, it has yielded satisfactory results.

The epithelial covering of the œsophageal mucous membrane consisted of numerous layers of squamous cells; the most superficial cells were much larger and more scale-like than those in the deeper layers, and presumably were more horny. The layer next the corium stained much more deeply with picrocarmine than those more superficially placed, but the shape of its cells could not definitely be ascertained. The corium consisted of connective tissue papillated on its free surface, and the papillæ were lodged in depressions in the deep surface of the epithelial covering. No glands were recognised in the œsophageal mucous membrane.

Sections through the mucous lining of the 1st gastric compartment displayed an abundance of tubular branched glands of the type of cardiac glands. The prevailing cells in the deeper part of these glands were the well-known large, ovoid, and spherical "peptic" cells, but in some sections remains of the smaller "axial" or "central" cells lying next the lumen could be seen. The cells occupying the parts of the gland tubes next the free surface were, like the epithelial covering of that surface, very much disintegrated, and a striking contrast was thus furnished between the more superficial, wider, and excretory part of the gland tube with its disintegrated epithelium, and the deeper more elongated secretory part loaded with "peptic" cells, which doubtless owed their preservation, so many weeks after the death of the animal, to the antiseptic properties of their contents.

Although Burmeister has not recorded a microscopic examination of the stomach of his Ziphioid, yet from his reference to the longitudinal folds of mucous membrane in the œsophagus, and the beautiful figure which he has given (plate xviii. fig. 4) of the mucous lining of the 1st gastric compartment, with its rounded convoluted folds, I have no doubt that structural differences existed between these mucous membranes similar to those which I have described in *Mesoplodon*. We have no proper microscopic examination of the 1st gastric compartment in

Hyperoodon, but Vrolik states that the œsophagus, with its mucous membrane elevated into longitudinal folds, possesses a semicircular valvular fold where it joins the stomach. There can, I think, be little doubt that in *Hyperoodon* the 1st gastric compartment will be found as a rule to resemble the corresponding cavity in the other Ziphioids. Eschricht's specimen of *Hyperoodon* furnishes, however, an important and remarkable exception to the arrangement. His 2nd compartment, from the size and the character of its mucous membrane, is obviously the same as the 1st compartment in Burmeister's Ziphius, Sowerby's Whale, my dried specimen of *Hyperoodon*, and probably those described by Jacob and Vrolik; whilst his 1st compartment is a comparatively small sac-like diverticulum from the œsophagus and with a similar epithelial lining.

It is obvious, therefore, that in *Mesoplodon* and in the Ziphioids generally the 1st compartment of the stomach is not a paunch-like diverticulum from the lower end of the œsophagus, lined by a squamous epithelium, as in the Delphinidæ, but is a true glandular digestive chamber. It is homologous, therefore, not with the 1st compartment of a Dolphin's stomach, but with the 2nd compartment, so that in the Ziphioids the paunch is not present. The paunch has either never been developed in this family of whales, or, what is more probable, it had existed at some remote period, and in the course of time it had become suppressed, though, as Eschricht's *Hyperoodon* shows, it may reappear as a variation in an individual animal. The direct communication between the œsophagus and both the 1st and 2nd gastric compartments in *Globiocephalus melas* will readily illustrate how, in the event of the suppression or disappearance of the paunch, the food would at once enter the next following compartment.

The question naturally arises, if the absence of the paunch in the Ziphioids and its presence in the Dolphins is correlated with differences in their food. The Dolphins, as is well known, are eaters of fish. Tyson long ago pointed out, that though there were no glands in the paunch of his Porpoise, yet that bones and other partially digested substances were found both in it and in the œsophagus,¹ and he surmised that gastric juice might regurgi-

¹ See Prof. Cleland's account of the paunch full of perfectly clean bones of the whiting in the stomach of the white-beaked dolphin (*L. albirostris*).

tate from the 2nd compartment into the 1st compartment so as to act upon the food lying in the latter. This view has been supported by Owen and other subsequent writers. *Hyperoodon* again lives largely, if not exclusively, upon Cuttle-fish. Of the food of Burmeister's *Ziphius* we know nothing, as its stomach was empty. Of the food of Sowerby's Whale I cannot speak with certainty, but it is possible that the crystalline lenses found in it may have been those of Cuttle-fish. The softness of the tissues of these cephalopods, and the absence of a bony skeleton, might render unnecessary, as a part of the economy of the Ziphioids, a chamber for the digestion of the harder tissues, such as is required by the Dolphins. On the other hand, the much greater number of compartments into which the Ziphioid stomach is divided, and the constricted valve-like openings between them, would of necessity greatly delay the passage of the food through the stomach, and, as my *Mesoplodon* showed, the harder and more indigestible materials were retained in the 8th and 9th compartments.

As regards the distal compartment in the stomach of the Ziphioids, it will be advisable, when suitable opportunities offer, to reexamine it and the commencement of the duodenum, as regards their general form, relations, and structure, and to compare them with those of the Dolphins, as it is not improbable that differences here also may be found in the two families.

We may now pass to the consideration of the stomach in other families of Cetacea, though unfortunately of them we have not the same fulness of information as we possess of the Dolphins.

The Sperm Whale (*Physeter macrocephalus*), which approximates in so many of its characters to the Ziphioids, possesses, according to the dissections of Dr J. B. S. Jackson¹ only three gastric compartments.

He states that the first cavity is nearly globular in form, and that it is lined by a continuation of the cuticle and cutis from the œsophagus. He did not apparently make a microscopic examination. The second cavity opens freely into both the œsophagus and 1st cavity. It is elongated, and the rugæ on its inner surface are nowhere strongly marked. The 3rd cavity is elongated, narrow at its commencement, but becomes dilated and curved upon itself. The mucous coat is less rugose than in the 2nd cavity. There is no small intermediate cavity between the 2nd and 3rd. The 3rd cavity opens

¹ *Boston Journal of Nat. Hist.*, vol. v., October 1845.

into a dilatation by an orifice $\frac{1}{4}$ inch in diameter. This dilatation ends in the intestine.

There is thus a great difference between the stomach of the Sperm Whale—which seems to be constructed more after the type of the Dolphins—and that of the Ziphioids, a circumstance which is the more remarkable when one remembers that *Physeter*, like *Hyperoodon*, lives largely upon Cuttle-fish. Some other factor, therefore, than differences in food requires to be considered in connection with the variations in the Cetacean stomach.

In the Platanistidæ the stomach of *Platanista gangetica* has been studied with great care by Dr John Anderson.¹

It possesses three distinct chambers, but consists chiefly of two large sacs (1st and 2nd compartments), placed side by side, and opening into each other by a common orifice at the termination of the œsophagus. The 2nd compartment leads into a short narrow passage or channel, that conducts to the 3rd compartment, which is only about one-eighth the capacity of the others, and of globular or oval shape. Succeeding the 3rd compartment is a globular cavity or dilatation, which Dr Anderson regards as an enlargement of the duodenum and not as a true gastric chamber. The 1st compartment is an elongated dilatation of the œsophagus, and is lined by stratified squamous epithelium. The 2nd compartment is lined by columnar epithelium, and richly provided with glands. The mucous lining of the 3rd chamber contains abundant glands similar to those at the pyloric end of the Pig's stomach.

In the arrangement and structure of the 1st and 2nd compartments *Platanista* presents a close resemblance to what I have seen in *Globiocephalus melas*, but the 3rd or distal compartment differs in form from that of the distal compartment in *Globiocephalus*, *Phocæna*, *Orcella*, and other *Delphinidæ*, in which it is very considerably elongated, and not globular as in *Platanista*. *Platanista* lives on both mud-frequenting fish and crustacea.

In the allied genus *Pontoporia blainvillii*, Burmeister has described² the stomach, from which it would appear that this organ consists of four compartments.

The first is melon-shaped, and with its mucous surface folded as in his Ziphioid already so frequently referred to, but the folds are relatively broader, less elevated, less numerous, and run in irregular undulations from its entrance to its outlet. The outlet into the 2nd compartment

¹ *Anatomical and Zoological Researches*, p. 441, plate xxvi., London 1878.

² *Proc. Zool. Soc. London*, 1867, and *Anales del Museo publico de Buenos Aires*, vol. i. p. 419.

is not at the end of the 1st compartment opposite to the œsophagus, but at the same side as the œsophageal opening; it is very narrow, and opens into a circular cavity 2 inches in diameter. The 3rd compartment is larger than the 2nd, but much smaller than the 1st, and is a prolonged oval in shape. The 4th is smaller than the 3rd, 2 inches long and 1 inch wide; it is separated from the 3rd by a narrow sphincter. The 4th ends in a tube, which soon widens into a sac $1\frac{1}{2}$ inch long and 1 inch wide, from which the intestine 144 feet long proceeds. This sac and the tube passing to it form the duodenum, for the pancreatic and hepatic ducts open into it at the point where the tube unites with the sac. The 1st compartment contained a fish (*Atherina argentinensis*) and some elytra of *Colymbetes*.¹

Of the Balænidæ, Knox possessed the stomach of a foetus of *Balæna mysticetus*, 2 feet $4\frac{1}{2}$ inches long.² This specimen is now in the Anatomical Museum of the University of Edinburgh, and I have drawn up from it the following description:—

The œsophagus was cut short and opened by a wide orifice into the 1st gastric compartment, which was about the size of a walnut. This opened by a wide orifice, situated not far from the œsophagus, and bounded by a fold of mucous membrane, into a 2nd compartment 2 inches long by $1\frac{1}{2}$ inch wide, which occupied the diameter of the stomach between the lesser and greater curvatures. Knox stated that a short canal on the concave margin of the stomach passed from the 1st into the 2nd compartment, but this appears to be only a constricted part of the latter. The 3rd compartment communicated with the 2nd at the end opposite the 1st; it was about the size of a small hazel nut, and it opened into the dilated commencement of the duodenum, into which the biliary and pancreatic ducts opened.

John Hunter³ and Drs Carte and Macalister⁴ have described the stomach in *Balænoptera rostrata* as possessing five compartments, though Mr Perrin says only four⁵:—

From Messrs Carte and Macalister's description the 1st compartment is oblong, and lined by a minutely convoluted mucous membrane; the 2nd communicates with the 1st, not far from the œsophagus. The 2nd (27 inches long) is much larger than the 1st, and sigmoid in shape. The valve-like opening between the 2nd and 3rd is 5 inches in circumference, and one of the same circumference is between the 3rd and 4th compartments, which are somewhat globular

¹ For the translation from the Spanish of Burmeister's description both of *P. blainvillii* and of his *Ziphius*, I am indebted to Mr James Gordon.

² *Catalogue of Anatomical Preparations, illustrative of Cetacea*, p. 21, Edinburgh, 1838.

³ *Op. cit.*

⁴ *Trans. Roy. Soc. London*, 1867.

⁵ *Proc. Zool. Soc. London*, Dec. 6, 1870.

in shape. The 4th is broadly pyriform, about $14\frac{1}{2}$ inches long. The 5th is only $9\frac{1}{2}$ inches long, and it opened into the duodenum through a small pylorus. Eschricht states¹ that in the Vaagewalls (*B. rostrata*) there are only three gastric compartments, but in a foetus $6\frac{1}{2}$ feet long he saw the 3rd (distal) compartment divided by four semicircular valves into five cavities. He says that both the oesophagus and the 1st compartment are lined by a thick epithelium, which terminates suddenly at the entrance to the 2nd compartment. Eschricht also describes the stomach of the Keporkak (*Megaptera longimana*) as consisting of three compartments, like that of *B. rostrata*.

Dr Murie has given² a description of the stomach of *Balænoptera musculus* (*Physalus antiquorum*).

It consists of four cavities. The 1st is globo-pyriform, and with a greater curvature of 99 inches; its mucous lining is slightly puckered, but near the greater curvature is elevated into polygonal folds; the openings of the oesophagus and of the 2nd compartment are situated on opposite sides of the lesser curvature. The 2nd compartment (97 inches long) is more cylindrical in form, and with longitudinal folds of mucous membrane. The 3rd cavity is 30 inches long, and the 4th 32 inches. The latter contracted at the intestinal outlet. The duodenum apparently has no dilatation, and the hepatic duct opens immediately beyond the junction of the 4th cavity with the intestine.

Both Cuvier and Meckel, as well as several later writers on the Cetacea, have endeavoured to establish a type number of compartments of the stomach in the various members of this important order of mammals. Meckel inclines to three as the type number, and Cuvier to five, and the latter anatomist is disposed to ascribe the discrepancies in the number stated by previous observers to some, regarding as a mere passage, what he would consider to be a cavity. But the *résumé* which I have given above of the description of numerous writers, as well as the special examination which I have made of *Mesoplodon*, have satisfied me that it is not possible to place in one simple type the numerical and morphological constitution of the Cetacean stomach. For, quite irrespective of such questions as to whether the compartment which I have numbered 3 in my figure of the stomach of *Globiocephalus* is a true gastric chamber, or only a passage, and whether the dilatation which I have marked 6 is gastric or duodenal, it is obvious that a tendency exists in the whales for a multiplication of compart-

¹ *Op. cit.*, p. 98.

² *Proc. Zool. Soc. London*, Feb. 14, 1865.

ments beyond either three or five, and that this tendency to multiplication is so pronounced that the number, by the formation of additional septa, may be larger in some individuals than in others of the same species. In the Ziphioids, as I have already stated, the compartments attain their maximum number, and from what I saw in Sowerby's Whale there was even an indication of the division of the 10th compartment into two smaller cavities. In Jacob's *Hyperoodon* there was one compartment more than in Vrolik's specimen, and in Eschricht's one more than in the animal described by Jacob. Eschricht again saw a specimen of *B. rostrata* with seven gastric chambers instead of five—the more usual number.

But, along with the tendency to multiplication in certain cavities, there also occurs in the Ziphioids a tendency to suppression of a particular chamber at the proximal end, viz., the 1st compartment or paunch of the Delphinidæ, though, as Eschricht's specimen of *Hyperoodon* shows, this compartment may appear in a rudimentary form in a particular individual. As to the presence or absence of a paunch in the Sperm Whale, the Platanistidæ, and Balænidæ, further information, based upon a microscopic examination of the mucous linings of the 1st and 2nd compartments in most of the species, is necessary before a positive statement can be made. Dr Anderson's account of *Platanista gangetica*, however, makes it quite clear that in that species the 1st gastric compartment resembles the œsophagus in its epithelial lining, and it is probable, from Eschricht's description, that a similar arrangement prevails in *B. rostrata* and *M. longimana*, so that they accord in this particular with the Dolphins.

Kidney.—Each kidney was 20 inches long and 5 inches in greatest width. It was divided into a number of small lobules, as is characteristic of the Cetacea.

Heart.—In removing the heart from the thorax, the fishermen had cut through both the auricles and the great arteries close to the base of the ventricles. The heart was flattened dorso-ventrally. The breadth across the base of the ventricles was $12\frac{1}{2}$ inches, from base to apex 9 inches. The wall of the right ventricle was $\frac{1}{2}$ inch thick at the base, and diminished to $\frac{1}{8}$ th inch at the apex. Strong columnæ carneæ projected from the inner

wall, and three of these projected as papillary muscles, the smallest of which was $1\frac{1}{2}$ inch, the largest 2 inches, in breadth at the base. Two papillary muscles were attached to the inferior wall of the ventricle, and one to the superior wall. The more posterior one attached to the inferior wall gave origin to two moderator bands, each of which was no larger than a piece of pack thread. They were connected by the opposite end to the septal wall; the more anterior was undivided, but the more posterior was divided into several fasciculi, which were attached close to the apex of the cavity. The septum was not oblique, but in the antero-posterior plane of the heart. The chordæ tendineæ were strong and attached to the flaps of the auriculo-ventricular valve, which consisted of three large cusps and of three intermediate cusps, which, though smaller, were still very well marked. The pulmonary artery had three large semilunar segments at its apex, and its mouth was 2 inches distant from the innermost cusp of the tricuspid valve.

The wall of the left ventricle was from $\frac{1}{2}$ inch to 1 inch in thickness. Two short muscoli papillares, $2\frac{1}{2}$ inches broad at the base, projected into the cavity, and were attached by chordæ tendineæ to the cusps of the mitral valve, which consisted of two large cusps, a superior and an inferior, and of two intermediate, very well marked, smaller cusps. The valve had therefore a quadri-cuspidate form. Two pea-like nodules were attached to the cusps of this valve. The endocardium was a little more opaque than on the right side. The aortic orifice was close to the mitral, being separated only by the more inferior of the two large cusps of the mitral valve. This orifice was guarded by three strong semilunar segments. From what remained of the auricular walls they had evidently possessed in the appendices elevated muscular bands, having a reticulated arrangement.

Lungs and Windpipe.—The *lungs* were somewhat flattened, from 26 to 28 inches in length, and from 6 to 10 inches broad. Apparently they were not divided into lobes, and each was invested by an opaque thickened pleura. Only the posterior end of the *trachea* had been preserved. It bifurcated into two large *bronchi*, but 5 inches above its bifurcation it gave off, as is the custom in the Cetacea, a large accessory bronchus, which entered the more anterior part of the right lung. The diameter

of the trachea immediately above this branch was 3 inches. The intrapulmonic part of the bronchi divided and subdivided on the dichotomous plan. The cartilages in the wall both of the trachea and bronchi were arranged sometimes annularly, but at others in a spiral direction. Not unfrequently they branched, and the branches might either unite with adjoining cartilages or terminate in free ends. The cartilages in the bronchi, of very fine calibre, were seen to go quite round the wall.

The *Larynx* was elongated at the summit as in other toothed whales. It had been cut across so high up that only a small part of the thyroid cartilage had been preserved, and the base of the epiglottis had been in part sliced away. The upper orifice had two thickened lips, the posterior projected somewhat higher than the anterior. The epiglottic cartilage formed the anterior boundary: it bifurcated at its thyroid end and between its two lateral halves, and the upper border of the thyroid was a shallow mesial pouch, lined by mucous membrane, which freely communicated with the interior of the larynx. This pouch had a fibrous wall externally, and outside that again were the remains of a thick muscle attached to the epiglottic cartilage. Owing to the imperfect condition of the larynx, I am not in a position to say if the cartilages, which formed the posterior wall of the elongated tube, were only the arytenoids, or if they consisted of arytenoids at the base, and of elongated cuneiform cartilages of Wrisberg at the upper end of the tube, as has recently been described by Mr G. B. Howes¹ in the Common Porpoise. Corresponding to the mesial border of the posterior cartilages was a longitudinal fold of the mucous membrane, which projected into the tube of the larynx; and at its upper end, where the anterior and posterior walls were in apposition, it was received into a corresponding depression in the anterior or epiglottic wall.

The presence of a laryngeal pouch in *Mesoplodon bidens*, in the interval between the epiglottic and thyroid cartilages, is interesting in connection with the observations on a corresponding arrangement by Dr Murie in Risso's Grampus,² and by Messrs Watson and Young in the White Whale.³ Murie regards

¹ *Jour. of Anat. and Phys.*, July 1880.

² *Ibid.*, Nov. 1870, vol. v.

³ *Trans. Roy. Soc. Edinburgh*, April 1879, vol. xxix.

this pouch as corresponding in kind, though of course very much smaller, to the great laryngeal sac which exists in the Whalebone Whales; and Watson and Young not only agree with Murie in this view, but, from the bilateral character of the laryngeal pouch in the White Whale, they also regard it as "homologous with the ventricles of Morgagni of other mammals, and that the enormous laryngeal sac of the Whalebone Whales must be equally regarded as their morphological equivalent."

FLIPPER.

The flippers had been disarticulated at the shoulder-joint, and the axial connections of all the muscles, blood-vessels, and nerves had been divided. I have drawn up the following notes on their arrangement from careful dissections made under my superintendence by one of my pupils, Mr Arthur Clarkson.

MUSCLES.—A strong tendon, which represented either the *teres major* or *latissimus dorsi*, or perhaps both muscles combined, was inserted into a vertical ridge on the flexor aspect of the humerus. Two muscles were inserted near the radial border of the humerus, the one, much the larger, into a tuberosity, and for some distance above it, the other into the bone nearer the flexor aspect of the limb; one of these muscles was probably the *subscapularis*. The tendon of another muscle was inserted into the extensor surface of the humerus in close relation to the origin of the outer head of the triceps; this was probably the *infra-spinatus*. The *triceps* was distinctly divided into three bellies, two arose from the shaft of the humerus, the third and largest was cut through, but had obviously arisen from the scapula; the bellies blended below and were inserted into the upper convex border of the olecranon.

Subjacent to the thin layer of blubber on the flexor aspect of the flipper, a strong aponeurotic membrane was exposed, the fibres of which ran in the long axis of the flipper. The upper end of this aponeurosis was continuous with the remains of what seemed to be a muscular belly, the origin of which had been cut through in the disarticulation of the flipper. This aponeurosis was attached below to the lower end of the radius, the lower end of the ulna, and the ulnar border of the carpus. When this aponeurotic tendon was reflected a strong fibrous membrane was

exposed which covered the deep flexor muscles, and which was attached above to the shaft of the humerus and to the olecranon, and below to the shafts of the ulna and radius. On removing this membrane three flexor muscles were exposed (Plate IV. fig. 2).

Flexor carpi ulnaris arose from both the olecranon and the adjacent part of the shaft of the ulna. The belly was $2\frac{1}{4}$ inches long and $1\frac{1}{2}$ inch at its widest part; it ended in a distinct tendon, which descended parallel to the hinder border of the ulna to be inserted into the pisiform bone of the carpus.

Flexor digitorum ulnaris arose from the lower end of the humerus, the olecranon, the shaft of the ulna, the ligament of the elbow-joint, and the interosseous septum. Its muscular belly was $6\frac{1}{2}$ inches long by $2\frac{1}{4}$ inches in its widest part, and gave origin to a powerful tendon, which descended obliquely towards the radial side of the wrist. This tendon was at first wide, then diminished in size, and again expanded prior to its division into three tendons, the most ulnar of which soon subdivided into two slips, which were inserted as low down as the terminal phalanges of digits V. and IV.

The tendon to digit III. ran undivided to have a similar insertion. The tendon to digit II. divided into two portions, of which the more radial part was inserted, by an expansion into the fibrous tissue, along the radial border of the manus, lower down than the short pollex; the other part was inserted mostly into digit II., but somewhat also into the fibrous tissue on the radial side of that digit.

Flexor digitorum radialis arose from the lower end of the humerus, from the radius and the interosseous septum. Its belly was only $2\frac{1}{2}$ inches long by 1 inch in its widest part, and from it a slender tendon proceeded, which gave off an expansion to the fibrous tissue which covered the carpal bones, also a slender slip to the tendon of the flexor digitorum ulnaris, and finally ended in the terminal phalanx of the pollex (digit I.) and in the fibrous tissue adjacent to it.

A muscular mass, 4 inches long by about $1\frac{1}{2}$ inch in its widest part, which was not so powerful as the muscular belly of the flexors of the digits, was situated on the extensor aspect of the flipper. It at first seemed to be a single muscle arising from

the ligament of the elbow, the radius, and the ulna; but when more carefully examined it appeared to be divided as follows into a radial and an ulnar portion by an inter-muscular septum:—

Extensor digitorum radialis gave origin to a tendon which almost immediately divided into two, for digits II. and III.; each passed down to the terminal phalanx of its digit; that to digit II. gave off several slips to the fibrous tissue of the radial border of the manus beyond the pollex and subjacent to the thin sub-tegumentary blubber; that to digit III. also gave some slips to the fibrous covering of its digit.

†: *Extensor digitorum ulnaris* gave origin to two tendons, one of which passed to digit V., to be inserted partly into it and partly into its fibrous covering; the other split into several slips which intercommunicated and again subdivided, some to end in digit IV. and its fibrous covering, others into the fibrous tissues between IV. and digits III. and IV. (Plate IV. fig. 3).

BLOOD-VESSELS.—The *Brachial Artery* was situated on the concave side of the humerus, and descended on the flexor aspect of the limb. It was placed in the interosseous interval between the flexores digitorum ulnaris and radialis and gave off *muscular* branches to them. It then appeared on the carpus immediately beyond the tendon of the flexor digitorum ulnaris, under cover of which it had previously been situated, and then bifurcated; one branch descended between digits II. and III., the other between digits III. and IV., and these *digital* branches were traced to the tips of their respective digits. When in the interosseous interval between the shafts of the radius and ulna, the main artery gave off a *perforating* branch, which passed between the two bones to the extensor aspect of the limb. This extensor or perforating branch then supplied *periosteal* twigs to the periosteal coverings of the radius and ulna, and a *carpal* branch which ran to the radial border of the limb, superficial to the joint between the radius and the first row of carpal bones, and gave off twigs to the periosteal covering of the carpal and metacarpal bones and phalanges. After giving origin to these branches the perforating artery descended to the dorsal aspect of the carpus, where it ended in four *digital* branches, which descended to the intervals between the five digits, one to each

interval; at the interval each branch bifurcated to supply the adjacent sides of the fingers.

Another vessel, an *ulnar artery*, the origin of which was cut across, was situated on the flexor aspect of the olecranon. It descended under cover of a strong fibrous band, which crossed the origin of the flexor digitorum ulnaris, then pierced this muscle, and appeared again in the interval between the flexor digitorum ulnaris and the flexor carpi ulnaris; it then descended parallel and close to the radial border of the carpus, where it sent off a branch to the ulnar border of the carpus, and then joined a carpal branch of the brachial artery, and the vessel formed by their junction descended in the interval between digits IV. and V.

Some veins were seen with the larger arteries.

NERVES.—Only one large nerve was seen passing to the flipper, the origin of which could not be ascertained. It apparently represented a *musculo-spiral* nerve. As it descended in the upper arm it gave a branch to each of the three heads of the triceps muscle. It continued to descend on the flexor aspect of the olecranon, and gave branches into the substance of the flexores carpi ulnaris and digitorum ulnaris. The branch to the flexor digitorum ulnaris probably gave an offset to the flexor digitorum radialis, although this branch was not traced. The trunk of the musculo-spiral nerve also gave origin to a large *perforating* branch, which pierced the arcuate fibrous membrane that connected the lower border of the olecranon to the shaft of the ulna. This perforating branch divided on the extensor aspect of the flipper into several twigs which entered the bellies of the two extensor muscles.

PERIOSTEUM, LIGAMENTS.—In the dissection of the flippers one observed the great strength of the periosteal covering of the bones and the continuity of the periosteum with the capsular ligaments of the elbow-joint and carpal series of articulations. Both the flexor and extensor tendons as they passed down the phalanges were retained in their place by sheaths formed by the strong fibrous covering of the digits, but they were freely movable within their sheaths. The cartilaginous part of the olecranon also possessed a thick perichondrium, continuous with an arcuate fibrous band, which descended from

the lower border of the olecranon along the ulnar border of the ulna as low as its carpal end. A strong fibrous band, continuous with, but partially differentiated from, the periosteal covering of the bones, was situated on the radial side of the extensor aspect of the carpus, and was prolonged down to the pollex to be attached to its metacarpal bone. It may possibly represent an aborted extensor muscle of the pollex.

Professor Flower was, I believe, the first to notice, but without describing, the presence of muscles and tendons in the fore-arm and manus of a Whalebone Whale (*Balænoptera musculus*).¹ In 1867 Drs Carte and Macalister gave a systematic description² of the muscles of the flipper in *Balænoptera rostrata*, and in 1870 Mr J. B. Perrin recorded³ his dissections of the muscles of the fore limb in the same species. In the winter session 1869-70, I dissected the muscles in the flipper of the foetus of the *Balænoptera sibbaldii* stranded at Longniddry.

The foetus was 19 ft. 6 in. long, and the flipper was 3 ft. 7 in. long, and although the animal had been dead for a considerable time, and the dissection was incomplete, I noted the following arrangements:—A *subscapularis* occupied the ventral surface of the scapula. An *infra-spinatus* and a *teres minor* passed from the dorsum of the scapula to the outer surface of the humerus. A *deltoid* passed from the acromion downwards to the humerus. A *triceps* was inserted into the olecranon process and its origin from the posterior border of the scapula was differentiated. A well-marked *extensor communis digitorum* arose from the lower end of the humerus, from the fibrous capsule of the elbow, and from the upper ends of the radius and ulna. It ended about the middle of the fore-arm in a strong tendon, which flattened out on the back of the carpus, and divided into four distinct tendons, each of which passed down the dorsal surface of its digit for some distance, when it became so incorporated on the one hand with the periosteum, and on the other with the deep surface of the skin, as to be differentiated with difficulty as a distinct structure. Two distinct tendons were seen on the flexor aspect of the fore-arm, between the radius and ulna, which were traced upwards to a muscular belly, which seemed to arise from the humerus and the fibrous capsule of the elbow. The larger and posterior tendon, which represented a *flexor digitorum ulnaris*, occupied its own sheath, and then expanded and divided into four distinct tendons, one for each digit. The smaller and anterior tendon, a *flexor digitorum radialis*, also in its own sheath, then divided into two tendons, which joined the tendons of the ulnar

¹ *Proc. Zool. Soc. London*, Nov. 28, 1865.

² *Trans. Roy. Soc. London*, June 20, 1867.

³ *Proc. Zool. Soc. London*, Dec. 6, 1870.

flexor going to the 1st and 2nd fingers: the tendon of the ulnar flexor going to the 1st finger being much smaller than that from the radial flexor. The tendons ended on the palmar surface of the digits like those on the dorsal surface. A musculo-tendinous mass, a *flexor carpi ulnaris*, arose from the olecranon, and passed along the inner border of the ulna to end in the spur-like pisiform cartilage.

The most detailed account of the muscles of the fore-limb in the whalebone whales has been given by Prof. Struthers in his descriptions of the flipper in *Balænoptera musculus*,¹ and in *Balæna mysticetus*.² In a note to his account of *B. musculus*, he refers to a dissection which he had made of the flexor and extensor muscles of the hand in *Hyperoodon*, and to the presence of a flexor carpi ulnaris in the Common Porpoise, and in November 1873 he gave a systematic description of the finger muscles in *Hyperoodon*.³ Dr John Anderson has described⁴ the muscles of the fore-arm and hand in *Platanista gangetica*, and in addition to a fairly marked flexor of the fingers, and a comparatively aborted extensor digitorum, he found two remarkable muscles, closely approximated together, which extended from the humerus and ulna along the ulnar border of the fore-arm to the border of the 5th metacarpal and the phalanges of digit V. He thought that one might represent an extensor, the other a flexor carpi ulnaris.

As might naturally be expected from the affinities between *Hyperoodon* and *Mesoplodon*, the arrangement of the muscles in Sowerby's Whale corresponded in most respects with what Dr Struthers had previously described in *Hyperoodon*, but there were some differences in detail; thus, whilst in *Hyperoodon* the flexor digitorum radialis ended in the radial tendon of the flexor digitorum ulnaris, in *Mesoplodon* it only gave a slip to the flexor digitorum ulnaris, and ended in the pollex and adjacent fibrous tissue, and the two divisions of the extensor mass appeared to have more independent insertions in *Mesoplodon* than in *Hyperoodon*.

It has been customary for authors to speak of the muscles in the fore-arm and manus of the Cetacea as rudimentary, and to

¹ *Jour. of Anat. and Phys.*, Nov. 1871, vol. vi.

² *Ibid.*, Jan. 1878, vol. xii.

³ *Jour. of Anat. and Phys.*, 1874, vol. viii. p. 114.

⁴ *Anatomical and Zoological Researches*, p. 542, London, 1878.

ascribe to them little if any function. Dr Struthers, to whose careful dissections of these muscles I have above referred, regarded them in *B. musculus* as having no more functional activity than would suffice "to give some rigidity or resistance to the joints, the tendons serving very much as ligaments which the muscles will help to tighten," and in the *Mysticetus* he regards their function as chiefly, if not altogether, ligamentous (p. 224); though in *Hyperoodon*, in accordance with the greater relative development of the muscles, and the greater mobility of the joints of the fingers and carpus, he considers that, to the merely passive resistance which a purely ligamentous condition would afford, these muscles will add some activity. Dr Anderson believes that the Gangetic Dolphin has considerable mobility of the manus, and especially that it has power over the fifth digit.

Undoubtedly, as all anatomists admit, the chief movements of the flipper in the Cetacea take place at the shoulder-joint by the action of the muscles inserted into the humerus; though I believe that the triceps, through its insertion into the olecranon, and through the very slight mobility of the elbow-joint, will also assist in drawing the entire limb backwards. As I have not dissected the muscles in the fore-arm and manus of a well-grown Whalebone Whale, I do not give an opinion on the extent of their action, though, from the highly cartilaginous condition of the carpus in these animals, I quite recognise that the skeletal arrangements would not admit of much mobility in the manus. But in *Mesoplodon*, as will be shown further on, the skeletal arrangements permitted of movements both between the carpal bones and at the joints of the digits themselves. I cannot, therefore, in this whale, look upon these muscles as having merely a ligamentous function, or as being rudimentary in the sense in which the short flexor muscle of the middle digit of the horse, and the short flexors of the middle and annular digits of the sheep and ox are rudimentary, when they become transformed into the suspensory ligament of the fetlock.¹ On the contrary, the red, fleshy bellies of these muscles, and the absence of fatty degeneration, the definite vascular and nervous

See Prof. D. J. Cunningham's very instructive paper on this subject in the *Jour. of Anat. and Phys.*, Oct. 1888, vol. xviii. p. 1.

supply, the mobility of the tendons in their sheaths, the presence of diarthrodial joints in the manus, all point to these muscles in *Mesoplodon* as being functionally active. When the flexors of the fingers were drawn upon, the phalangeal and metacarpal part of the manus was bent towards the fore-arm, so that a certain amount of palmar flexion was permitted. But, owing to the preponderance in size of the flexor digitorum ulnaris, the direction obliquely towards the radius both of its muscular belly and of its tendon prior to its division, and the greater relative size of the tendon going to digit II., the radial border of the hand was also bent towards the ulnar border, so that the entire manus was not only flexed, but an oblique or somewhat rotatory movement was communicated to it, such as is given to an oar in the act of "feathering." The extensor muscles were not so powerful as the flexors, but, upon being drawn upon, they straightened the digital part of the manus after it had been flexed, and also bent it very slightly towards the dorsum of the fore-arm. The elasticity of the cartilaginous structures in the manus, and the resistance offered by the water, would during life co-operate with the extensor muscles in this action and render it unnecessary for them to be so powerful as the flexor muscles. Owing to the five digits being enveloped in a common tegumentary covering, movement of the individual digits was not permitted, but the thinness of this covering allowed the movements of the manus to which I have just referred. The feathering movement of the hand would without doubt and to the efficiency of the flipper as an instrument of progression.

The distribution of nerves to the anterior extremity of *Mesoplodon* is, as regards the number of trunks, more simple than was observed by Professor D. J. Cunningham in his dissections of the Porpoise and *D. albirostris*.¹ In these Delphinidæ, in addition to the nerves supplying the muscles acting directly on the shoulder-joint, a medio-ulnar and a musculo-spiral trunk were described by that anatomist. With the exception of a branch from the latter nerve to the triceps muscle, these nerves, owing to the absence of muscles in the fore-arm, were distributed to the skin of the limb. But in *Mesoplodon* only a single nervous trunk was seen, which, after supplying the triceps, gave

¹ *Jour. of Anat. and Phys.*, vol. xi.

branches to both the flexor and extensor muscles in the fore-arm; probably also it supplied the skin of the fore-arm and hand, although the cutaneous nerves were not traced.

SKELETON.

As I have on former occasions described the character of the skull of a female¹ *Mesopiodon bidens*, and the skull and a large part of the skeleton of an adult male,² it is not necessary to describe the entire skeleton of this male specimen. It will be sufficient if I point out, along with the most salient features, some differences between this and the preceding male, and describe those bones which were missing in that specimen. The skeleton was fully ossified, all the epiphyses being united.

Skull.—The maximum length of the skull was 30 inches, and the beak, from the premaxillary foramen, was $20\frac{1}{8}$ inches long. The beak tapered very elegantly in front, and terminated with the tips of the premaxillary bones. The meso-rostral (medio-rostral) canal was to a considerable extent, as in my previous male, which I shall call No. 1, occupied by a meso-rostral (medio-rostral) bone, which extended 12 inches in front of the mesethmoid and ended in a point, but was not, as in No. 1, longitudinally grooved on its upper surface. As this bone was not present in the female skull, it marks a sexual character. The greatest breadth of the skull, between the post-orbital processes, was $12\frac{1}{4}$ inches; the greatest height of the skull from pterygoids to vertex was $10\frac{3}{4}$ inches. The malar was a very slender bar, attenuated at its temporal end, but plate-like anteriorly.

The mandible was $26\frac{1}{2}$ inches long, and the characteristic pair of mandibular teeth projected for nearly 2 inches beyond the alveolar border. They were placed partly opposite and partly behind the posterior end of the elongated symphysis. The two halves of the mandible could not be separated from each other, as they were ankylosed at the anterior end of the symphysis.

The tympano-periotic bones were intact. The tympanic bone had the bilobed form inferiorly and posteriorly, which has been

¹ *Trans. Roy. Soc. Edin.*, May 20, 1872.

² *Proc. Roy. Soc. Edin.*, Jan. 30, 1882, and *Jour. of Anat. and Phys.*, April 1882.

described by Professor Flower¹ in *Mesoplodon australis* and *grayi* and by myself² in a young *M. layardi*. I have compared it carefully with the tympanic of Layard's *Mesoplodon*. They had both the same length, $1\frac{8}{10}$ ths inch; but the maximum breadth in Layard's whale was 1.4 inch and in Sowerby's 1.2 inch. In Sowerby's whale the outer lobe was not so rounded, and the groove between it and the inner lobe was not so deep, but it extended more distinctly to the anterior end of the bone than in Layard's whale. The inner surface in Layard's whale, where it passed to the entrance into the tympanic bulla, turned abruptly from the inferior surface; but in Sowerby's whale the inner and inferior surfaces passed gently into each other by a rounded border. The outer surfaces were very similar in the two specimens, but the vertical groove in Sowerby's was a little wider than in Layard's *Mesoplodon*, and the mastoid part of the bone, which was continuous with the tympanic by a constricted neck, was a little more elongated than in Layard's whale. The petrous bone in Sowerby's whale was $1\frac{1}{8}$ ths inch long and $1\frac{1}{8}$ th inch in greatest breadth, so that its dimensions were not quite so great as those of Layard's *Mesoplodon*; but in their general form and appearance the two specimens closely corresponded. A sharp spur-like process descended from the squamous-temporal immediately in front of the petro-tympanic, and prevented displacement forwards of these elements of the temporal.

The *Hyoid apparatus* consisted of a body (basi-hyal) and pair of great cornua (thyro-hyals), conjoined into a single hyoid bone, a pair of cerato-hyals, and a pair of stylo-hyals. Both the body and great cornua were flattened, and although the general form of the bone was concave upwards, yet the great cornua themselves were convex on their upper surface. The great cornua tapered slightly to the tip, and the distance between the tips of the two horns was $7\frac{1}{2}$ inches, the greatest antero-posterior diameter of the horn was $1\frac{1}{2}$ inch, and the greatest antero-posterior diameter of the body was $1\frac{1}{4}$ inch. The cerato-hyals were each $1\frac{1}{4}$ inch long, and were cylindriform rods of cartilage movable both on the hyoid and the stylo-hyals; they

¹ *Trans. Zool. Soc. London*, vol. x. part ix., 1878.

² *Challenger Reports*, part iv., 1880.

were attached to the hyoid so close together that the interval between them was a mere chink. The stylo-hyals were almost parallel to the great cornua, and on each side an *inter-hyoid* muscle occupied the whole length of the intermediate interval. Their inner ends, where they were jointed to the cerato-hyals at an acute angle, were 1 inch asunder; their outer ends, 10 inches asunder, were tipped with cartilage, and attached by a strong ligament to the under surface of the mastoid temporal. The greatest antero-posterior diameter of each stylo-hyal was $1\frac{1}{2}$ inch; the inferior surface was marked by a ridge running from within outwards, but the upper surface was concave in its inner half.

Spine.—The vertebral formula was $C_7, D_{10}, L_{11}, Cd_{19}=47$. It possessed, therefore, one vertebra more than is present in the skeleton at Brussels, and in each of the two skeletons in the museum at Göteborg. It agreed with No. 1 in the number of vertebræ in the cervical, dorsal, and lumbar regions, but as in No. 1 several caudal vertebræ were missing, I cannot compare it in that region. It had the same number of cervical and dorsal vertebræ as in the Brussels and the first of the Göteborg specimens, but it had one lumbar more than in the Brussels and two more than in the first Göteborg skeleton. The terminal caudal vertebra was no larger than a big pea, and, if I had not received the tail entire, would in all probability have been lost.

The atlas and axis were ankylosed into a single block; the remaining cervicals were separate bones. The laminæ of the 3rd, 4th, 5th, and 6th were not united mesially, but the 7th had an elongated spine. No cervical had a complete vertebrarterial foramen.

In the dorsal vertebræ the mesial ridge appeared on the inferior surface of the 9th vertebra. The anterior six dorsals were, as regards their costal articulations, the same as in No. 1. The 7th had no definite costal facet on either side of its body; it had the strong articular process for the tubercle of the corresponding rib projecting from the side of the pedicle close to the zygapophysis. It is to be regarded as the vertebra of transition. The 8th, 9th, and 10th dorsals had no articular surface for the rib on the side of the neural arch, but a transverse process' for articulation with the rib, which, whilst a mere ridge in the

8th, increased to $3\frac{1}{2}$ inches in the 10th, projected from each side of the body.

Eleven vertebræ intervened between the last dorsal and the first vertebra which carried a chevron bone, so that we must speak of eleven lumbar vertebræ. There were nineteen caudals, which diminished in size from before backwards, the terminal one being no larger than a big pea, but jointed by a distinct disc to the penultimate vertebra, so that it was movable.

A vertical foramen appeared in the 7th caudal at the root of the transverse process, and was seen in the sides of the bodies of several succeeding vertebræ. The caudals in front of the 7th were grooved on the side of the body behind the transverse process for lodgment of vessels. There were eight chevron bones; the vertical diameter of the longest was $7\frac{1}{4}$ inches and of the shortest $1\frac{1}{2}$ inch.

Ribs.—Ten pairs of ribs were present, which is the normal number in this species, although the second Göteborg skeleton had only nine pairs of ribs. The 1st to the 7th inclusive each had a head, neck, and tubercle, and possessed therefore two vertebral articular surfaces. The 8th, 9th, and 10th had a single articular surface only for the transverse process on the side of the body. The length of the 1st rib in a straight line was $12\frac{1}{4}$ inches; of the 2nd, $18\frac{3}{4}$ inches; of the 3rd, 23 inches. The 6th and 7th were the longest ribs, each being between 26 and 27 inches long. The 10th rib was the shortest, and was only 11 inches long. The shafts of the more anterior ribs were broadened out in proximity to the tubercle, and concave on the pleural surface.

Sternum.—The sternum was a flattened bone $22\frac{1}{2}$ inches long. It consisted of five segments—the 3rd, 4th, and 5th being ankylosed together, the 1st and 2nd separating during maceration. The 1st segment was prolonged forward into two elongated cornua, between which was a deep presternal notch. These presternal cornua were very short in No. 1. Four mesial foramina were in the bone; that between the 3rd and 4th segments was no bigger than would admit a quill, whilst the others were of considerable size. This bone articulated laterally with six pairs of ribs.

Pelvic bones.—These bones had been removed along with the penis and its muscles, but both muscles and penis had been much

injured. Each bone was a slender curved bar, concave inwards, convex outwards, the right was $3\frac{1}{2}$ inches long in a straight line, the left scarcely $3\frac{1}{2}$ inches; the greatest breadth of the bone was about $\frac{1}{2}$ inch, the posterior end of each bone was pointed, and tipped with a thin layer of cartilage, the anterior end formed a rounded tubercle, the transverse distance between the outer curved aspects of the two bones was $5\frac{1}{2}$ inches. A muscle was attached to the outer aspect of each bone, but was cut through so that its outer attachment could not be seen. A broad thick muscle, *erector penis*, arose from the inner aspect of each bone, and passed forwards and inwards, partly to join its fellow in the mesial line, and partly to be attached to the strong fibrous wall of the crus and corpus cavernosum penis. Behind it was another thick muscle, so much injured that its attachments could not be determined. When the erector was removed the crus penis was exposed, and its attachment to the inner concave surface of the pelvic bone, to a little more than its posterior third, was seen. The body of the penis, as is usual in the Cetacea, was not divided into two corpora cavernosa. The corpus spongiosum urethrae was imbedded in the under surface of the body of the penis, and the urethral tube within it was no larger than would admit a moderate-sized porcupine quill. Between the urethra and the strong fibrous envelope of the corpus spongiosum was erectile tissue. The penis was 17 inches long from the attachment of the crus to the anterior pointed extremity of the organ.

Anterior Extremity.—The *scapula* was somewhat larger than in No. 1. The elongated bar-like coracoid and the groove-like pre-spinous fossa were well marked. The *humerus* was $6\frac{1}{2}$ inches long, with a flattened shaft, and a large head covered with cartilage. The *radius* and *ulna* had the usual flattened form in the Cetacea, and were arranged side by side. The radius was $6\frac{1}{2}$ inches long between its upper and lower articular surfaces, and the ulna was $5\frac{3}{4}$ inches. The ulna had a large bony olecranon, which ended in a cartilaginous prolongation 2 inches long, the olecranon mounted by the side of the shaft of the humerus to within $1\frac{1}{2}$ inch from the head of that bone. The elbow-joint was enclosed by a dense strong capsule. When cut into, the ends of the bones were seen to be encrusted with

cartilage, and to bound a joint cavity containing synovia. A slight joggling movement seemed all that was possible at this joint.

The *manus* was pentadactylous. The *carpus*, when compared with the Whalebone Whales, consisted of a maximum of bone and a minimum of cartilage. The cartilage, indeed, except near the pisiform, was no greater in amount than sufficed to encrust the articular surfaces of the bones. The carpus was made up of a proximal row, a distal row, an *os centrale*, and a pisiform.

The proximal row contained three bones—*radiale*, *intermedium* and *ulnare*. The *radiale* (scaphoid) was one inch in transverse

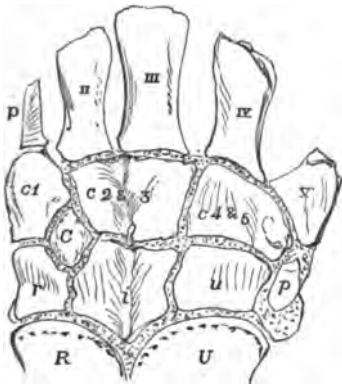


Fig. C.

FIG. C.—The palmar or flexor surface of the *Manus* (without the phalanges) of *Mesoplodon bidens*. *R* and *U* the lower ends of the radius and ulna; *r*, *radiale*; *i*, *intermedium*; *u*, *ulnare*; *p*, *pisiform*; *c* 1, *carpale* 1; *c* 2 and 3 represents apparently the 2nd and 3rd *carpalia*; *c* 4 and 5 represents apparently the 4th and 5th *carpalia*; *C*, *os centrale*; *P* *pollex*; II. to V. the *metacarpals* of the four fingers.

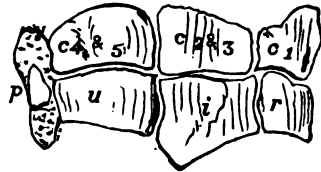


Fig. D.

FIG. D.—The extensor or dorsal surface of the carpal bones of the same animal; the lettering is the same.

These figures and figure E have been drawn from the specimens by my son, Mr W. A. Turner.

diameter and articulated with the radius, *intermedium*, *centrale*, and *carpale* 1. The *intermedium* (*lunare*), $1\frac{1}{2}$ inch in transverse diameter, was grooved on its flexor aspect for the tendon of the flexor digitorum ulnaris; it articulated with the radius, ulna, *radiale*, *ulnare*, *centrale*, and the bone representing *carpalia* 2+3. An important feature in its arrangement was the ascending process, which it sent upwards between the lower ends of the

radius and ulna, to articulate with both bones. The ulnare (cuneiform), was $1\frac{1}{2}$ inch in transverse diameter and articulated with the ulna, intermedium, pisiform, and the bone representing carpalia 4+5.

The distal row consisted of three bones, of which the most radial was the trapezium or carpale 1 of Gegenbaur, the next in all probability represented carpalia 2+3, and the third similarly represented carpalia 4+5. Carpale 1 (trapezium) was one inch in diameter, and articulated with the radiale, centrale, the representative of carpalia 2+3, and the metacarpals of pollex and II. Carpalia 2+3 (conjoined trapezoid and magnum), formed a single bone $1\frac{1}{2}$ inch in transverse diameter, which was grooved on its flexor aspect for the tendon of the flexor digitorum ulnaris; it articulated with the centrale, intermedium, carpale 1, with the bone representing carpalia 4+5, and the metacarpals II. and III. Carpalia 4+5 (unciform) formed a single bone $1\frac{1}{8}$ ths in transverse diameter, which was grooved on its dorsal surface opposite the interval between metacarpals IV. and V.; it articulated with the ulnare, pisiform, the bone representing 2+3 carpalia, and metacarpals IV. and V.

The centrale was only visible on the flexor aspect of the carpus, where it projected slightly as a roundish nodule, 0.6 of an inch in its longest diameter. It was wedged in between the proximal and distal rows, and articulated with the radiale, intermedium, carpale 1, and the bone representing carpalia 2+3; it passed for some depth into the substance of the carpus, but did not appear on the dorsal aspect. The pisiform was almond shaped, nearly an inch in its long diameter, and was placed quite on the ulnar border of the carpus. It articulated with the ulnare and with the bone representing carpalia 4+5, and a prolongation of the cartilage which surrounded it was sent upwards to the lower end of the ulna, and downwards to metacarpal V.

The radiale was separated from the radius, and the ulnare from the ulna, by distinct joint cavities, with synovial fluid, but the intermedium was attached to its articular surfaces on the radius and ulna by intermediate cartilage, which tore through when the bones were drawn asunder, and a similar attachment was between the intermedium and the radiale on the one side and the ulnare on the other. A diarthrodial joint

cavity, with synovial fluid, was interposed between the distal and proximal carpal rows. The distal carpalia were partly connected to each other by intermediate cartilage, but in part this cartilage was hollowed out into small joint cavities.

The pollex consisted of a slender cylindriform metacarpal bone, and an elongated nodule of cartilage which represented an unossified phalanx. Digit II., which was slightly the longest, consisted of a metacarpal bone and five phalanges; Digit III. contained a metacarpal bone and four phalanges; Digit IV. a metacarpal bone and three phalanges; Digit V. a metacarpal bone and two phalanges. The metacarpals of the fingers were flattened, and this was especially seen in the short metacarpal V., which was also set at an angle to metacarpal IV. The phalanges were movable on the metacarpal bones and on each other, and had apparently joint cavities in the intermediate cartilage.

A figure of the carpus in Sowerby's whale has already been given by Dr A. W. Malm,¹ but it differs in several particulars from the carpus which I have just described. It possesses in the proximal row the radiale, intermedium, and ulnare, though Malm interprets the radiale as if it were compounded of both scaphoid and trapezium. In the distal row it has C 1 (trapezium), C 2 (trapezoid), C 3 (magnum), C 4+C 5 conjoined to form an unciform. Malm interprets C 1 as if it were the metacarpal bone of the pollex, whereas from its position it is obviously, as in my specimen, the first bone of the distal carpalia. It will be observed also that whilst in my specimen a large bone represents both C 2+3, in Malm's they are distinct as a trapezoid and a magnum. In Malm's the pisiform is not ossified, and there is no os centrale. M. van Beneden, in his description of the skeleton of the female Sowerby's whale in the Royal Museum in Brussels,² states that the two rows of the carpus have each three bones, of which the middle is the largest. M. Gervais states³ that in the skeleton of this whale from Sallenelles, preserved in the museum at Caen, there are three proximal carpals and three distal carpals.

¹ *Hvaldjur i Sveriges Museer ar*, 1869, plate v. fig. 52, Stockholm, 1871.

² *Mém. de l'Acad. de Belgique. Coll.*, in 8vo, tom. xvi.

³ Van Beneden and Gervais, *Ostéographie des Cétacés*, p. 401

In my specimen, being an adult male, the ossification of the carpus had reached a more advanced stage than in any previously described example, for not only were certain bones in the distal row, which had probably arisen from originally distinct centres conjoined, but it had both an ossified pisiform and an os centrale. In the possession of an os centrale it recalled the well known type-form of carpus of Gegenbaur as figured by him in the manus of the Water Tortoise (*Chelydra serpentina*). So far as I have been able to ascertain, no example of an os centrale has previously been described in the Cetacean carpus, though its presence in the carpus of the Orang and some other mammalia is universally recognised. In the human carpus also a cartilage, which represents it, has been described both by Rosenberg and by Kölliker at an early stage of development in the young embryo, and as has been shown both by Wenzel Gruber and by myself,¹ it occasionally persists as a distinct ossicle in the adult human carpus. It is interesting to note that in the adult human carpus which I described, the os centrale, as in Sowerby's whale, was visible on one aspect only of the manus, but whilst in the cetacean it was seen on the flexor aspect, in the human manus it appeared on the dorsal surface.

Another character in the carpus of this *Mesoplodon*, which also deserves attention, is the prolongation of an ascending process from the proximal surface of the intermedium into the interval between the lower ends of the radius and ulna. From Malm's figure of his specimen I have little doubt that a similar arrangement occurred in it also, though he does not refer to it. In Gegenbaur's figure of the carpus of *Chelydra* the intermedium is also represented as prolonged into an interval between the bones of the forearm, an arrangement which doubtless shadows out the true position of this bone in the forelimb. Professor Marsh, in his description of the limbs of *Sauranodon* (*Baptanodon*)² points out that, in the hind limb of that reptile, three bones articulate with the lower end of the femur, and he regards the middle of these three as the intermedium; whilst the two others are tibia and fibula. He considers that the true position of the intermedium is in this the epipodial segment, and that

¹ *Journ. of Anat. and Phys.*, p. 246, vol. xvii., 1883.

² *American Journal of Science*, pp. 170, 491, vol. xix., 3rd series, 1880.

in the specialisation of parts in the higher vertebrates it is gradually crowded out of that segment into the mesopodial or tarsal segment, where it is usually found. In the hind limb of many birds the astragalus possesses an ascending spike-like process which passes into the interval between the tibia and fibula. In the present number of this *Journal* (Oct. 1885) Mr J. Bland Sutton directs attention to some observations by Professors Wyman and Morse¹ on the tarsus of birds, in which it was recognised that the spike-like process arose from an independent centre of ossification, and Mr Sutton confirms these observations by an examination of an embryo cygnet and an ostrich chick. Both Morse and Sutton consider this spike-like process to correspond with the os intermedium of the typical tarsus, and they have both figured in the amphibian salamander an ascending process of the intermedium passing into the interval between the tibia and fibula. Now, if this fundamental position of the intermedium is true of the hind limb, it is without doubt also the case in the anterior extremity, and the intermedium in it is in all probability originally a member of the fore-arm or epipodial segment.

The light which this carpus in Sowerby's whale has thus thrown upon the constitution of the mammalian carpus has led me to study this part of the Cetacean skeleton in some other specimens of natural skeletons of the manus in the Anatomical Museum of the University. One of the most interesting of these is a carpus which, though unmarked, obviously belongs to the skeleton of an adult *Hyperoodon rostratus*. The proximal row consists of radiale, intermedium, and ulnare. The intermedium has only a short ascending process. The distal carpalia are five distinct bones, not so regularly faceted as those in the proximal row, and with a larger proportion of cartilage between them. These bones pass from the radial to the ulnar border in regular order, as C 1 to C 5, and each is associated with the metacarpal bone of its corresponding digit. A similar arrangement exists in both hands. The carpus possesses also an elongated pisiform cartilage, which in one hand is partially ossified (fig. E).

This is, I believe, the only specimen of a mammalian carpus in which the presence of five distinct carpal bones has been re-

¹ *Anniversary Memoirs*, Boston Soc. Nat. Hist., 1880.

cognised in the distal row. M. Gervais has indeed figured¹ the manus of a foetal *Hyperoodon* in the Museum in Paris, in which he represents five cartilages in the distal row, and in his description he states that one is for each finger, but that the 5th of these "faisant saillie," juts out, like a pisiform. A skeleton in the Museum at Lille has also, he says, the same number of carpals. Apparently, therefore, he regarded the most ulnar of these cartilages not as a distal carpale, but as a pisiform. The position of these bones in my adult carpus, and of the corresponding cartilages in the foetus figured by Gervais, leaves no

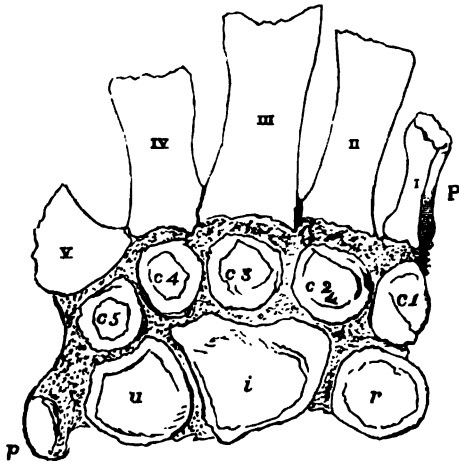


FIG. E.—Surface of Manus (without the phalanges) in *Hyperoodon rostratus*.
The lettering as in fig. C.

doubt in my mind that we have here to deal with five distal carpalia, such as Gegenbaur has figured in *Chelydra*; and that the carpus in *Hyperoodon* exhibits, therefore, in this particular, the generalised arrangement of the carpalia seen in that reptile; but it does not possess an os centrale. The carpus of *Hyperoodon*, figured by Vrolik,² had only four bones in the distal row, one for the pollex and one for each of the three succeeding digits. The minimus had no distal carpal, but from the large proportion of cartilage in this manus it is obvious that the animal was not adult, and the ossific nucleus for carpale 5 had not yet been formed.

¹ Van Beneden and Gervais, *Ostéographie des Cétacés*, pl. xliii. fig. 4, p. 373.

² *Op. cit.*, pl. iii.

As regards the carpus in *Ziphius cavirostris*, an example of which has been figured by A. W. Malm (pl. v. fig. 51), I differ from that anatomist in the interpretation to be put on the bones. Those of the proximal row are, I believe, ulnare, intermedium, and radiale, and the last named is not, as he conceives, a scaphoideo-trapezium. Those of the distal row, four in number, are, I believe, an unciform (carp. 4, 5), an os magnum (carp. 3), a trapezoid (carp. 2); whilst the most radial bone in this row, which he regards as the metacarpal of the pollex, is in my judgment a trapezium (carp. 1). From Burmeister's figure of the carpus (plate xviii. fig. 2) of his *Ziphius*, it would appear that it possesses radiale, intermedium, and ulnare; but only three bones in the distal row, a trapezium for the pollex, trapezoid for the index, a magnum (carp. 3, 4) for both medius and annularis, and that carpale 5 has not been formed.

In the right natural carpus of a well-grown *Globiocephalus melas* in the University Museum the following bones were seen:—In the proximal row, radiale, intermedium, and ulnare, the last named being much the smallest. The intermedium had a distinct ascending part between the radius and ulna, so that nearly one-half the intermedium lay below the lowest points of the radio-ulnar surface.¹ In the distal row there was no carpale for digit V., the metacarpal bone of which was set at such an angle as to articulate with both the ulnare and the inferior epiphysis of the ulna. The most ulnar distal carpale articulated with metacarpals IV. and III; it probably represented carpale 4. Next in order was a carpale which articulated with metacarpals III. and II., and was probably carpale 3. Then followed a carpale which articulated with metacarpal II., and was without doubt carpale 2, and was situated at the radial border of the carpus. On its distal aspect was a rounded bone 0·7 inch in diameter; which was also at the radial border of the manus, and in longitudinal series with the phalanges of the pollex. In transverse series it was in the plane of the proximal ends of the metacarpal bones of the fingers, and has usually been regarded as the metacarpal bone of the pollex. In its rounded form and roughened surface it is much more like a distal carpal than a metacarpal, and

¹ The proportion of intermedium between the two bones of the fore-arm was like that which Gegenbaur figures in *Menopoma* (pl. i. fig. 6).

I am disposed to regard it as carpale 1 (trapezium). The elongated bones in the pollex distal to the rounded bone would therefore be a metacarpal and two phalanges. If this view be correct, then *Globiocephalus* has four distal carpals and not three as is usually stated. In this carpus the proximal articular surfaces of metacarpals II., III., IV. were bi-faceted, like the lower end of the humerus, and the facets were separated by an intermediate ridge; the distal carpalia articulating with them were therefore pushed laterally, so as not to lie opposite the ridge, but to articulate with the lateral facets, and therefore intermediate to two metacarpals. But, in addition to these bones, an osseous nodule was embedded in a piece of cartilage, which occupied the interval between the radiale, intermedium, carpale 2, and carpale 3; from its position it represented an os centrale. In the left carpus the os centrale was absent, though the corresponding cartilage was there, and the ulna was fused with the distal carpale, which I have numbered 4. No pisiform was present in either manus.

The observations which I have made on these specimens have led me to form a somewhat different conception of the constitution of the carpus in the Toothed Whales than has been customary. It is obviously of importance to study this part of the skeleton in adult forms, and with the bones and cartilages in their natural position, and not artificially articulated. Whilst the specimens confirm the view that three bones make up the proximal row, they also show that the general statement frequently made that only three bones occur in the distal row is not applicable to all the species. In *Hyperoodon*, for example, there are five distinct distal carpalia in the fully ossified skeleton, and in a younger animal, like Vrolik's specimen, four distal carpalia. In *Ziphius cavirostris*, also, I hold that there are four distal carpalia, and I put the same interpretation on the distal portion of the carpus of *Globiocephalus*. In *Mesoplodon bidens*, again, a definite os centrale occurs in the adult carpus, and even in *Globiocephalus* this carpal element sometimes appears. The pisiform bone is found also in *Mesoplodon* and *Hyperoodon* in addition to the examples given by Professor Flower¹ in *Physeter*, *Inia*, and *Delphinus tursio*.

¹ *Trans. Zool. Soc. London*, vol. vi., 1868.

The diminution of the number of the distal carpalia, from the type number five, may be due either to one or more centres of ossification not having formed in the carpal cartilage, or to the fusion with each other of ossific nuclei, which were distinct in the younger condition of the same carpus. Diminution by non-formation of a distal carpal is well seen in *Globiocephalus*, in which metacarpal V. has no distal carpal to articulate with, and consequently that digit is set further upwards than is usual, and approximates to the ulna and to the proximal row; also in Vrolik's *Hyperoodon* in which, from not being an adult, carpale 5 had not yet formed. Because the pollex is feeble in the Cetacea, and has a tendency to disappear, it was thought by van Bambeke¹ that the trapezium was frequently not developed, even when the rudiments of a pollex were present, and both he and A. W. Malm have put into the metacarpal series a bone which I have regarded as carpale 1(trapezium). Diminution by fusion of two carpalia is seen in my *Mesoplodon bidens*, in which the most ulnar bone in the distal row had a groove on its dorsal surface opposite the interval between metacarpals IV. and V., which indicated, I believe, the line of fusion of two originally distinct bones. But a bone in the proximal row may also fuse with one in the distal row, as in the left carpus of *Globiocephalus*, in which the ulnare is fused with carpale 4, whilst on the right side they are distinct. I am not, however, disposed to hold with A. W. Malm that the bone, which in so many of his figures of the carpus, he calls a scaphoideo-trapezium, is a combination of these two carpal elements from different rows. On the contrary, I regard it as the radiale (scaphoid) only, and consider the bone which, in many of his specimens, lies immediately on its distal side, to be the trapezium. I do not, however, maintain as a universal proposition that, when a distal carpal in the Cetacea articulates with two metacarpals, it has necessarily been produced by the fusion of two originally distinct centres of ossification, as it may have arisen from only a single centre, which, either by suppression of a centre on one or the other side of it, or by a limited growth of such a centre, has extended laterally in the cartilaginous matrix so as to articulate with more than one metacarpal bone.

That the anterior extremity of a Cetacean is much more

¹ *Mém. de l'Acad. Roy. de Belgique*, t. xviii., 1865.

generalised in many of its characters than it is in other mammals is well known. The flattened form of the bones of the fore-arm, with the radius fixed in the cephalic edge of the limb; the multiplication of the phalanges in several of the digits; the simplicity in form of the metacarpal bones and phalanges, and the difficulty in distinguishing these from each other, except by their relative size, are at once apparent. But my observations on the carpus in the specimens described in this paper have brought out that in this part also of the skeleton a more generalised plan of construction prevails than is customary in mammals. The presence of five distal carpalia in *Hyperoodon*, the tendency of the intermedium to pass between the radius and ulna in *Mesoplodon* and *Globiocephalus*, are arrangements which call to mind Gegenbaur's figure of *Chelydra serpentina* and Marsh's of *Sauranodon*, and show that in these respects also the anterior extremity in these Cetacea exhibits a less amount of departure from the more primitive form of carpus than is customary in mammals. Even the occurrence of an os centrale in *Mesoplodon* and in *Globiocephalus*, which, though not without its homologue in many other mammals, is of interest also in the same particular.

EXPLANATION OF PLATE IV.

For the drawings of natural size from which these figures were reduced, I am indebted to one of my pupils, Mr A. C. Harkness.

Fig. 1. Dorsal surface of tail of *Mesoplodon bidens*.

Fig. 2. Flexor aspect of dissected flipper. *n*, musculo-spiral nerve; *b*, brachial artery; *u*, ulnar artery; *fc*, flexor carpi ulnaris; *fu*, flexor digitorum ulnaris; *fr*, flexor digitorum radialis; *P*, pollex.

Fig. 3. Extensor aspect of dissected flipper. *n*, musculo-spiral nerve; *tr*, triceps; *ol*, olecranon; *er*, extensor digitorum radialis; *eu*, extensor digitorum ulnaris; *pn*, perforating nerve to extensors; *pa*, perforating artery to dorsum of hand; *P*, pollex.

Notices of New Books.

The Anatomy of the Intestinal Canal and Peritoneum in Man. By FREDERICK TREVES, F.R.C.S., *Hunterian Professor at the Royal College of Surgeons of England, Surgeon to and Lecturer on Anatomy at the London Hospital.* (4to. H. K. Lewis, London.)

THIS work consists of the lectures delivered at the Royal College of Surgeons in 1885, and gives the results derived from the systematic examination of one hundred fresh bodies, besides fetuses and lower animals. The average length of the small intestine in the adult male is found to be 22 feet 6 inches, in the female 23 feet 4 inches; of the colon, 4 feet 8 inches in the male, and 4 feet 6 inches in the female. The length is independent of age, height, and weight, and the ratio between large and small intestines is not constant; the differences in length being referable to physiological rather than morphological data, that is to say, to the nature of the food, the vigour of the digestive processes, &c. At birth the small intestine is 9 feet 5 inches, and the large 1 foot 10 inches. This is singularly constant; but after birth the growth of the small intestine proceeds in an irregular manner, which has probably relation to the irregularities and varieties of diet in children, especially among the lower classes.

A particular account is given of the *fossa*, and the *plica duodeno-jejunalis* in the peritoneum, near the commencement of the jejunum, with their development and relation to retro-peritoneal hernia; also of *mesenteric holes*. These he finds to be most common near the termination of the ilium, where the ileo-colic branch of the superior mesenteric artery circumscribes, by its anastomosis with the last of the intestinal arteries, an area on the mesentery, of a well-rounded or oval shape. This area presents no fat or blood-vessels. The peritoneum in its becoming atrophied and cribriform a hole is easily made here, perhaps, by a knuckle of bowel which may become strangulated.

A laborious investigation proved that it was impossible to determine such a localisation of the coils of the small intestines as to enable the surgeon to form a notion of the part of the small intestines that would be likely to be involved in each of the various herniæ on different sides of the body. For instance, "it is not uncommon to find loops lying together in contact with the pelvic floor that are in reality some 12 or 14 feet apart, as may be seen when their proper position in the course of the bowel is defined" (p. 33). It is an important point in connection with the relation of the mesentery to hernia that if the "condition of the viscera and peritoneum be normal, it will be found

impossible to drag a loop of small intestine through the femoral canal (artificially enlarged) on to the thigh, or down the inguinal canal into the scrotum. In fact, no coil can, in any part, be drawn out of the abdomen below a horizontal line on a level with the spine of the pubes. It is evident, therefore, that in a femoral or a scrotal hernia the mesentery must be elongated" (p. 27). Mr Birkett, the author remarks, has called attention to this subject, but its importance appears to have been overlooked.

With regard to the relations of the cæcum, the author finds the result of his investigations to be entirely at variance with the statements contained in the anatomical text-books. Instead of being, as usually stated, destitute of peritoneal covering behind, and attached by areolar tissue to the fascia covering the right iliacus muscle, in every case that he "has yet seen the cæcum has been entirely enveloped on all sides by peritoneum, and has been free in the abdominal cavity" (p. 40). It is connected by the reflection of the peritoneum or commencement of the meso-colon, commonly with the psoas muscle, rarely with the iliacus, and in some instances it is free from both muscles and hangs over the pelvic brim, or is lodged entirely within the pelvic cavity. These relations are, of course, of great interest both in surgery and medicine, and indicate the impossibility of carrying into effect certain operations upon that organ which have been proposed. His observations also respecting the relative frequency of the presence of a mesocolon on the two sides are not in accordance with the statements in surgical text-books, for he finds that a mesocolon may be expected upon the left side in 36 per cent. of all cases, and on the right side in 26 per cent. His observations, also, do not quite accord with the received account of the anatomy and relations of the sigmoid flexure of the colon and the rectum. The remarks respecting the ileo-cæcal fossæ, the cæcal folds, and other points are of much interest; but it will be sufficiently evident from the points to which we have alluded that Mr Treves has made a valuable contribution to our knowledge of the anatomy of the intestinal canal and the peritoneum. The work is illustrated by twenty-two figures.

Old Age and Changes Incidental to it. By G. M. HUMPHRY, M.D.,
F.R.S. (Cambridge: Macmillan and Bowes.)

THIS was the annual oration delivered before the Medical Society of London, May 4, 1885. The results given in it, which relate chiefly to the condition of the costal cartilages, the arteries, the rate of the heart's beat and of respiration, the atrophy of the bones, the loss of teeth, &c., are derived from 500 returns made to a schedule of inquiries issued by the Collective Investigation Committee of the British Medical Association, of which Professor Humphry is the chairman. The stages and processes of old age and decline are regarded as physiological and developmental processes of a "descending" development, quite as much as those of the "ascending" development of early life, and they take place, unless interrupted, in as regular and as duly proportioned a manner, so as to maintain the requisite working balance between the several organs. "Yet, strange and paradoxical as it may seem, this gradual natural decay and death, with the physiological processes which bring them about, do not appear to present themselves in the ordinary economy of nature, but to be dependent upon the sheltering influences of civilisation for the opportunity to manifest themselves and to continue their work." In the pure realm of nature "death is swift, and comes early, as soon, at least, as failure of strength renders the animal unable to protect or provide for itself; and man, it would seem probable, in early periods, had no exemption from this sharp, though, on the whole, beneficent law of animal life." Thus the prolongation of life into the periods of decay and also disease are attributed to civilisation; and it is the further work of civilisation to combat and root out disease, and to give the body the best opportunities for health and longevity.

The reparative powers exhibited by the aged in the repair of wounds and fractures, to which the author called attention in the preceding volume of this *Journal*, are mentioned, many confirmatory facts having, in the interim, been communicated by various members of the profession; and the orator concluded by stating that there are many points in relation to longevity which remain to be discussed, and asked for further information from those who have the opportunity of making returns respecting persons who have attained to great age.

Frozen Sections of a Child. By THOMAS DWIGHT, M.D., *Parkman Professor of Anatomy at Harvard University.* (Wm. Wood & Co., New York.)

THE subject was the body of a girl, three years old; and as the anatomy of this age has received little attention, and the peculiarities due to the age are carefully noticed in the text, the work is of much value, especially as the plates are of life-size, and drawn from the sections with much care. For instance, in the section through the abdomen and loins, the following are among the points observed:—The spinal cord has come to an end near the top of the third lumbar vertebra, whereas in an adult woman it terminates about half-way down the second, and in man about the lower border of the first, so that the cord is still relatively long. The umbilicus is opposite the fourth lumbar vertebra, i.e., a little lower than in the adult. There is one of the invaginations of the small intestine which probably often occur in children without giving rise to any symptoms. The cæcum has not made much progress in its descent from the right hypochondrium; and Professor Dwight's observations lead him to think that the wanderings of the cæcum are not completed so soon as authorities state. He believes that, as a rule, it does not reach its permanent position till a year or two after birth.

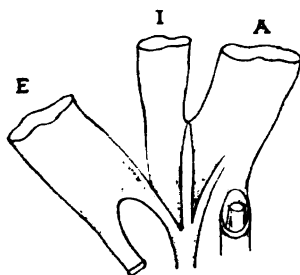


Fig. 1.

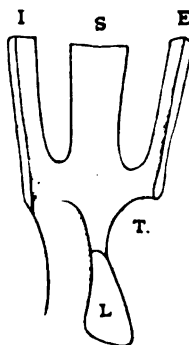


Fig. 2.

Fig. 3.

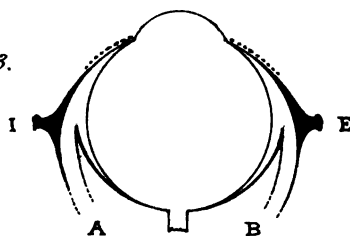


Fig. 4.

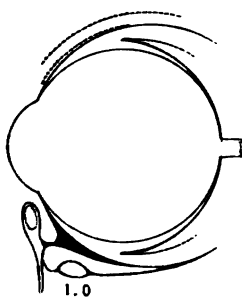
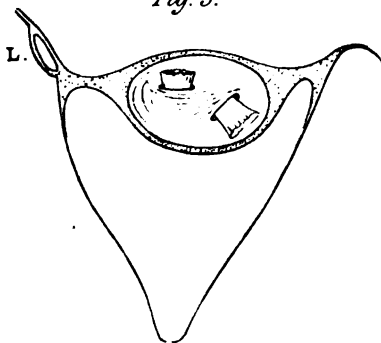
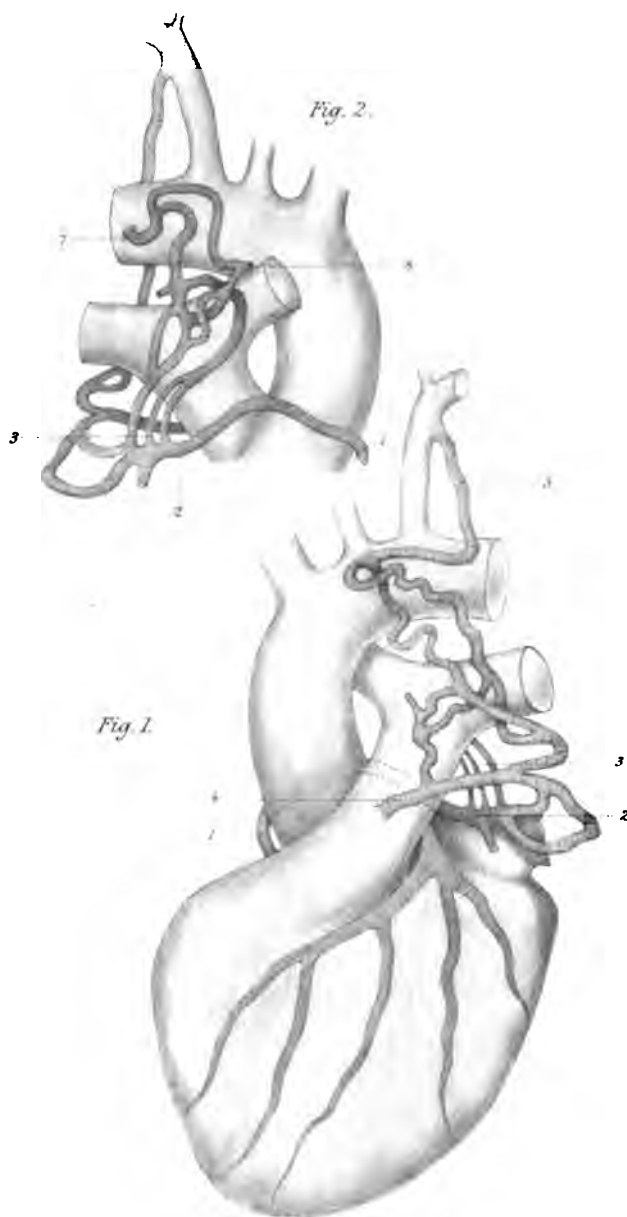
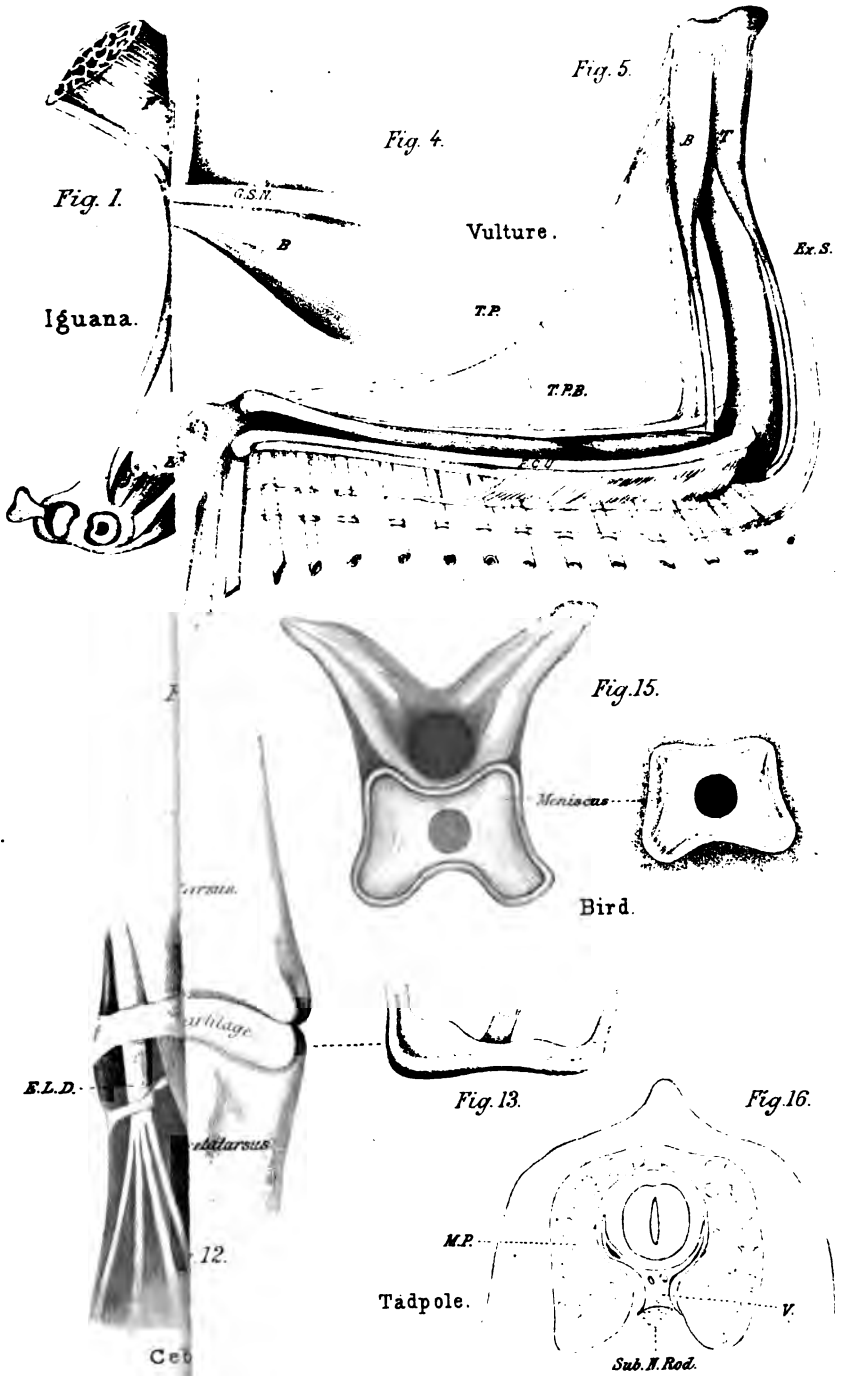
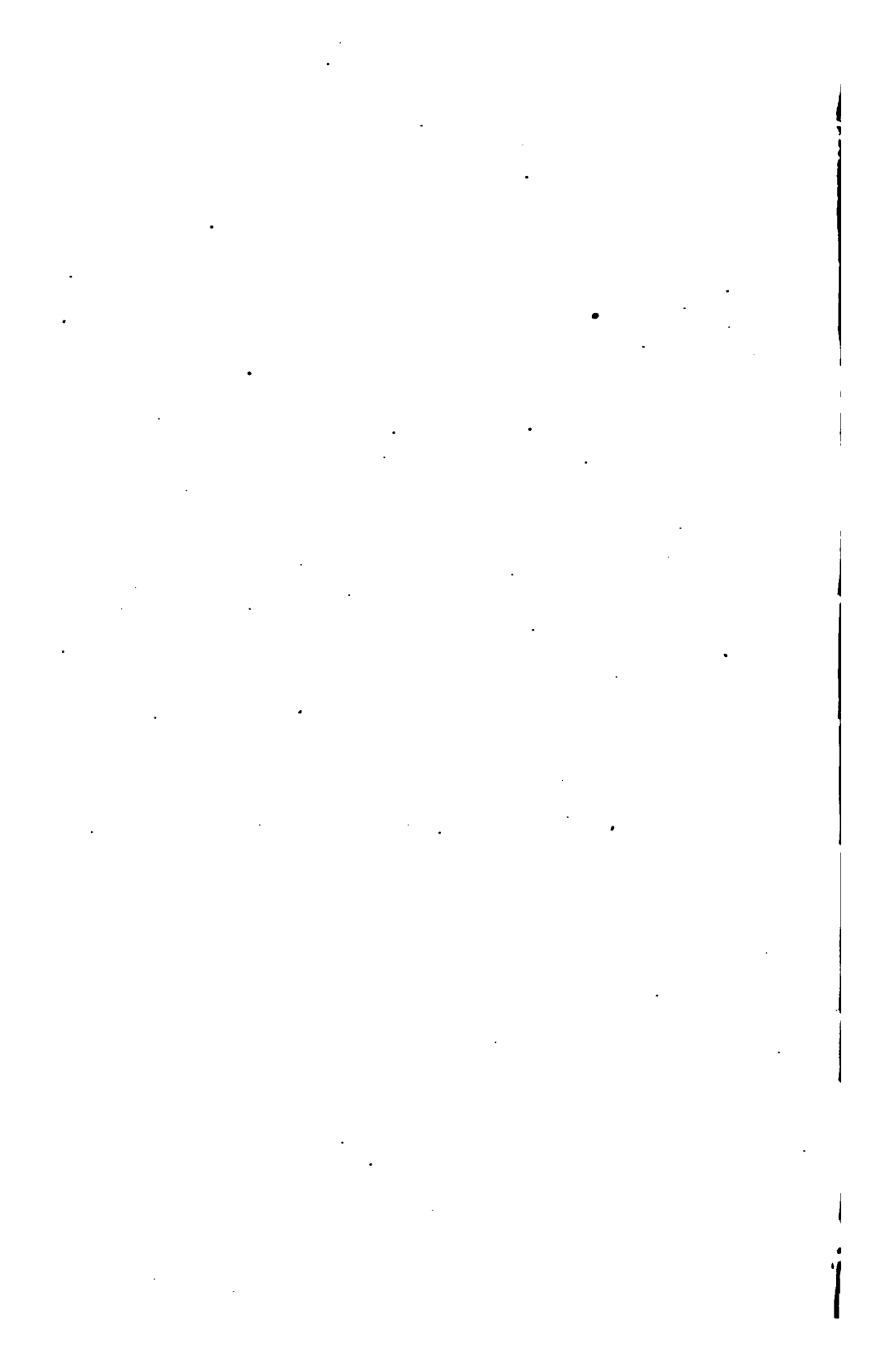


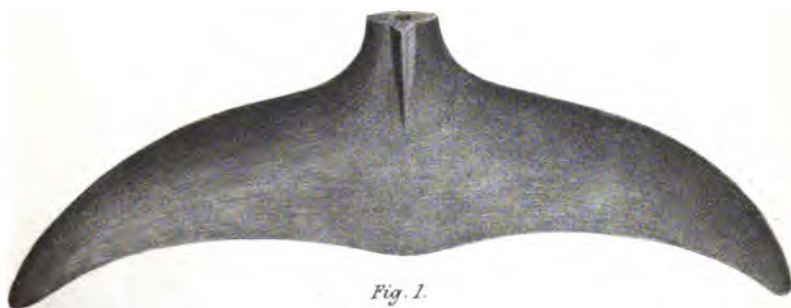
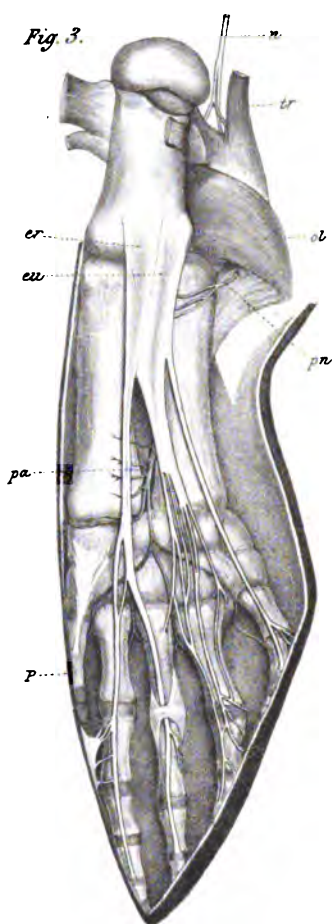
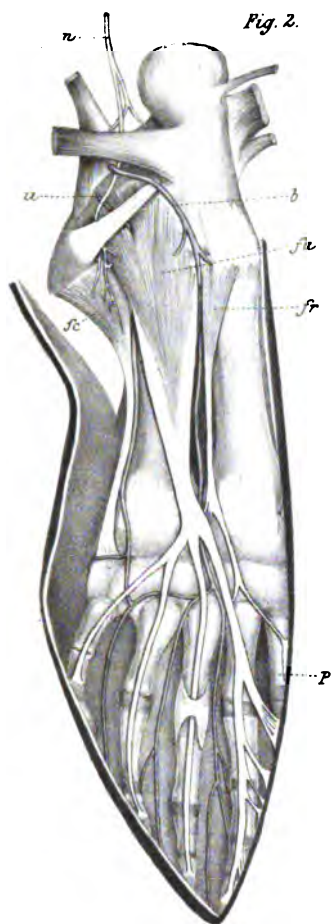
Fig. 5.











Journal of Anatomy and Physiology.

THE MORPHOLOGY OF THE ARTERIAL SYSTEM IN MAN. (PART I.) BY A. MACALISTER, M.A., M.D., F.R.S., *Professor of Anatomy, University of Cambridge.*

THE arrangement of the blood-vessels in the adult forms of the lowest, and in the embryos of the higher vertebrates, indicates that the history of the complicated vascular system of higher forms has been one of development from a simple and regular ancestral condition of metameric and inter-metameric vessels, through easily defined stages, to the more confused and irregular condition of the arterial system in the adults of higher forms.

The blood-vessels participate in the metamerism of the vertebrate body, however that metamerism may have arisen; but as the vascular system arises in the course of the increasing division of labour of the organism for the transport of nutriment from one part to another, the chief stems are those which are dia- or inter-metameric. The simplest vertebrate vascular system probably consisted of a tubular arcade or half ring on the splanchnic wall of each segment on each side, joined to the corresponding arch in the preceding and succeeding segment by a dorsal and ventral inter-metameric trunk on each side of the median line. In the whole organism the vessels would thus form a double series, two long ventral trunks, two corresponding dorsal trunks, and the lateral uniting arches in each segment.

One of the earliest changes which took place in this primitive system, was the fusion into single trunks of the longitudinal vessels. There are two primitive dorsal vessels in vertebrate embryos, and their fusion can be traced in the chick, beginning at the forty-second hour of incubation. This union commences behind the head and travels backwards rapidly, so that after the

fifth day there is but a single dorsal vessel for the middle and hinder part of the body—the dorsal aorta.

In the region of the head and neck in mammals, the foremost ends of the two vessels remain permanently separate as the internal carotid arteries, while the part intervening on each side, between the united vessels forming the aorta and the separated parts forming the carotids, called on each side *Ductus Botallii*, becomes obliterated, except in cases, like those described by Harrison, Quain, and Flood, in which the persistence of the ductus and the obliteration of the transverse part of the third aortic arch causes the internal carotid to arise independently from the aorta. I saw one unilateral instance of this some years since, in Dublin, which, like the other described case, was on the right side.

There were also originally two ventral longitudinal vessels, but their union probably occurred even earlier than that of the dorsal. This embryonic doubleness of the ventral stem has been regarded as a secondary cleavage, due to the presence of food yolk, but, I think, on insufficient evidence.

The setting apart of one portion of the single ventral vessel to form the heart differentiates the pre- from the post-cardiac portions of the ventral vessel. The latter becomes venous, and we shall not at present trace its history farther. The former becomes the ventral aorta.

The adult arterial system consists of the modified pre-cardiac ventral vessel, the dorsal trunk, the pre-cardiac lateral arcades, and the dorsal portions of the metameric vessels in the post-cardiac segments, together with new branches arising from these.

As a consequence of the cardiac differentiation, the only places where complete metameric arcades remain are the pre-cardiac segments, where the ventral aorta is joined to the dorsal by vessels which become the lateral aortic or branchial arches.

Behind the heart in higher vertebrates, a series of vessels extend from the dorsal aorta through the mesogastric fold, and end in the splanchnopleure; these correspond to the dorsal extremities of the post-cardiac lateral metameric arcades, but just as the pre-cardiac lateral vessels have become specialised by the development of the branchial clefts into respiratory arches, so these, very early in the phylum, have participated in the specialisation of the post-cardiac splanchnopleure and become

visceral arteries. Like their anterior representatives, they become broken into a rete in the middle of their course, forming a capillary plexus, and from this their ventral continuation has become venous, ending in the sub-intestinal ventral vein, the specialised derivative of the post-cardiac ventral vessel. The modified remains of these vessels we know in human anatomy as bronchial, œsophageal, coeliac, mesenteric, and vitelline arteries, which, originally paired, have for the most part undergone, like the longitudinal trunk, a fusion into single median vessels. If these were completed they would stretch from the dorsal to the ventral vessel, but the causes of their displacement and of their being cut short are easily seen.

On the development of the muscle plates, a parietal branch from the dorsal aorta arises in each metamere for its supply, and when the muscular wall of the somatopleure differentiates into dorso-lateral and ventro-lateral muscles, this vessel gives off corresponding dorso-lateral, and ventro-lateral branches. The former of these extends into the tissues arising from and below the laminae dorsales on each side, the latter extends ventrally into the somatopleure.

These metameric parietal branches from the dorsal aorta are not necessarily similar in size and distribution, although serially homologous in origin, for, like all smaller vessels, they arise, for the convenience of the segment, to supply the needs of the developing parts; they also are not necessarily regular, their evolution being proportional to the sizes of the territories to be supplied, and to the activity of the metabolism therein.

The metameric parietal branches are least modified in the region of the thorax, where they form the inter-costal arteries, also in the loins, where they form the lumbar vessels, each single trunk on each side giving off dorsal and ventral branches.

The terminal branches of the dorso-lateral vessels form a continuous series of inter-segmental anastomoses along the closed edge of the dorsal fissure on each side, which becomes in the adult the posterior spinal artery, receiving supplies from the entire series of segmental vessels. A similar but late-forming and single median anastomosis forms along the floor of the dorsal groove, the anterior spinal artery. Free anastomosis along this region is necessary, as the spinal cord requires a constant,

uniform, and uninterrupted blood supply. The ventro-lateral branches likewise form along the medio-ventral line on each side a chain of medio-ventral anastomoses; these become, in the adult, the epigastric and internal mammary arteries.

Coincidentally with the development and consolidation of the separate parts and processes of the axial skeleton different systems of inter-metameric anastomoses arise. These vary in position and size according to the general principle which regulates all such anastomoses, viz., that whenever a primitive blood channel is so placed that its blood stream is liable to be interrupted, communications form between its branches and those of neighbouring trunks at the nearest spot where there is the minimum of pressure or displacement. In the dorsal region, owing to the development of the rib-basket and the consequent intersegmental immobility, the parietal trunks are not liable to much compression, so, except at their ventral terminations, the anastomoses are small.

Watching the development of blood-vessels, we learn with what facility vessels form in mesoblast, and although I cannot speak positively, yet from what I have seen I think it probable that vessels have proceeded in development from the compound lacunar system to the tube; it is also probable that, historically, vascular space has at first arisen in the excavation of single plastides by *diacelosis*; and when, in the course of descent, a trunk has become established, the process is then abbreviated as we find it in the chick, where in the formation of large trunk vessels the space arises by the liquefaction of the central cells of primitively solid cords.

The largest inter-metameric anastomoses of the parietal vessels take place close to their primary divisions, the dorso-lateral trunks communicate by smaller or larger branches on the dorsal surface of the rib, between the rib-neck and the front of the transverse process; these ante-neural junctions are the chief regular communications, but others occur more irregularly and opistho-neurally. The chief radical anastomoses of the ventro-lateral branches is precostal. Each ventro-lateral artery gives off also a larger or smaller lateral branch close to the exit of the lateral spinal nerve, which is superficial in its distribution.

Each dorso-lateral artery in the thoracic and lumbar region having communicated, although by very minute vessels, with its

preceding and succeeding segmental representative, divides into internal and external branches, the former being the lateral spinal, which ends in the inter-metameric anterior and posterior spinal anastomoses; the latter ends in the dorso-lateral muscles. Each ventro-lateral branch in the thoracic and anterior four lumbar segments of man, pursues also a uniform course, having a very small precostal anastomosis and a fairly uniform segmental distribution.

The parietal branch belonging to the lower cervical, lower lumbar, and upper sacral segments are much disturbed in their simplicity by the development of the limbs. As these arise by the consolidation of ventro-lateral appendages derived from several segments, so each limb primarily receives vessels as it receives nerves from several metameric trunks; but, coincidentally with the reduction of the basipterygium to a single rod we have a corresponding reduction of the main arteries to a single or at most a double trunk, which, in accordance with a well-known law of vascular distribution, runs along that side of the limb which is the least exposed to pressure, and least liable to alteration in length in the course of accustomed movement. The vessels which become enlarged to supply the limbs are the lateral branches of the ventro-lateral trunks; we have seen that there are such branches, although extremely minute in all segments, but they are specially large in such segments as have contributed to the formation of the limbs.

The parietal branch of the last cervical segment is the trunk subclavian, arising from the dorsal aorta, above the point where fusion into a single trunk ceases, and as these constitute the chief blood supply of the fore-limbs they are commensurately large. Each gives off as its postero-lateral branch the *cervicalis profunda*, and these, like their serial homologues, pass backwards and give off lateral spinal branches inwards, and muscular branches outward.

Owing to the alteration in the dorsal aorta consequent on the retrocession of the heart, the trunk parietal artery for the first thoracic segment is obsolete at its root, but this is compensated for by the development of a large precostal anastomosis from the preceding trunk, which, on the principle that "to him that hath shall be given," not only thus supplies the appended limb,

but by this channel forms the functional root of the first, sometimes also (by the enlarging of the second precostal intermetameric anastomosis), of the second intercostal arteries, the whole distributional system arising from this anastomotic root being named the *superior intercostal* artery. It is rare to find a direct union of this vessel with the aorta, but I have twice seen it to arise therefrom on the left side, and once from the bifurcation of the *arteria innominata*, that is from the right aorta. Tracing the subclavian trunk a little further forward, it terminates at the inner edge of the *scalenus anticus* muscle. Its posterior medio-ventral anastomotic branch passes backwards as the internal mammary, its lateral branch pierces the *scaleni*, the cervical equivalents of the intercostal muscles as the so-called second stage of the subclavian artery, which is thus morphologically differentiable from the first stage.

In the more anterior cervical region, the vascular system of the component segments is necessarily much modified. The metameric arches are displaced backwards, and the portion of the dorsal aorta from which the parietal vessels should arise, the *Ductus Botalli*, is obliterated, hence the blood supply must be provided for by anastomosis. To this end a large retro-costal intersegmental anastomosis ascends from the root of the parietal vessel of the last cervical segment; this enters the interspace between the sixth and seventh cervical segment, and is, in the young foetus, placed at its origin at this level; but as the heart recedes and pulls all the cervical vessels downwards, its root becomes displaced ventrad of the seventh cervical rib (anterior root of the seventh cervical transverse process). This large anastomotic trunk ascends retro-costally but ante-neurally, giving off at each segment lateral spinal, and muscular branches precisely in series with those of the trunk segments. This trunk vessel is the vertebral artery, the first stage of which is the portion due to cardiac displacement, the second stage being the regular intersegmental union.

On reaching the first cervical segment, the continuous anastomosis is interrupted, so the whole vessel here divides into the two proper to the segment, a muscular outgoing, and a large lateral spinal ingoing, which, like its predecessors, turns inwards to the spinal cord, ventrad of the spinal nerve, which, owing to

its large size, it overlaps; here it joins the two longitudinal anastomoses, the posterior or posterior spinal, which, from its disproportionate size, looks like a branch of this lateral spinal stem, and the anterior or median or basilar, which is the continuation forwards of the anterior spinal system, the lozenge-shaped space from between the basilar and the anterior spinal being an island, similar to which I have thirteen times seen similar islands bounded by divisions and reunions of the basilar trunk.

It is thus interesting to see how, in the course of the vertebral artery, we have so diverse morphological elements represented, the retrocostal, intersegmental anastomosis constituting its first and second stages, and the large lateral spinal branch of the first cervical segment constituting its third and fourth stages. Thus we have the complete system of dorso-lateral branches for the cervical segments provided in the absence of a dorsal aorta.

When we take into consideration the varieties of position and course of the vertebral artery in man, and its apparently discrepant relations in elasmobranch, teleost, reptile, and bird, we find that this view of its nature enables us, in the simplest manner, to explain all its variations, and makes us understand why this system should be so prolific in varieties.

The ventro-lateral parietal branches of the cervical segments are also united by a continuous precostal anastomosis, not far from where their origins had originally been from the now obliterated aortic trunk; this anastomosis constitutes the thyroid axis and cervicalis ascendens, from which the modified ventro-parietal branches start. These are chiefly remarkable as giving off lateral branches, which contribute their quota to the nutrition of the limbs, as the suprascapular and posterior scapular; their parietal branches are small; the posterior branch of the former and the superficial cervical branch of the latter are the contigued parietal branches of these two trunks.

With the condensation of the anterior segments which takes place in the formation of the skull, all distinct vascular metamerism is lost, and the anterior segmental arches become displaced backwards or obliterated. The common and external carotids are the continuations of the ventral aorta, while the root of the internal carotid is the altered relic of the third arch, and the ascending continuation of that vessel is the upper part

of the dorsal aorta. The length of the carotids is secondary, as is the length of the neck upon which it depends.

In the region of the oral and pre-oral visceral clefts, the branches of the stem arteries are distributed in superficial and deep branches to the ventral parts of each inter-fissural tract of tissue; thus to the infra-hyoidean region we have, as superficial and deep branches, the superior thyroid and superior laryngeal arteries; to the supra-hyoidean we have the hyoidean artery, and more deeply the lingual; to the mandibular region we have superficially the facial, deeply the ascending palatine artery; to the maxillary lobe we have externally the transverse facial, internally the internal maxillary, to the fronto-basal lobe we have the temporal.

None of these branches are the vessels of visceral arches; they are secondary medio-ventral anastomoses, uniting the widely separated representatives of the ventral aortic trunks. The only carotid branches which in any measure represent rudimental arcades are the occipital and posterior auricular arteries.

The cervical dorsal aortic (internal carotid) has only rudimental branches in the neck, represented by the intercarotid ramuli. Its intracranial continuation gives off three lateral neural branches, the posterior, middle, and anterior cerebrals (the first originally being a carotid branch, its root being the so-called posterior communicating, but its anastomotic internal branch, which joins the median anastomosis, dilates so as to form its functional root). The ventro-lateral branches are reduced and modified as tympanic, vidian, receptacular, and ophthalmic branches. Upon all these branches the characters of the secondary alterations which the cranial segments have undergone have thus impressed themselves, so as to obliterate all traces of primitive segmentation.

THE ANATOMY OF THE SHOULDER AND UPPER
ARM OF THE MOLE (*Talpa Europæa*). By R. AUSTIN
FREEMAN. (PLATE V.)

THE increasing interest in Morphological Science which has of late years become manifest among scientific men has led to the careful examination of the structure of a large number of individual forms, and to the publication of detailed descriptions of their anatomy.

These contributions to Anatomical Science frequently contain matter which in itself is of considerable interest, and which, in the hands of the morphologist, forms the material for important generalisations.

It is somewhat curious that amidst this great activity of anatomical research, one of the most specialised and aberrant, although at the same time most archaic, of our British mammals should have been passed over in comparative silence, and the more so as the difficulty of obtaining specimens for examination is so very slight. It is true that notices of the anatomy of the mole have from time to time appeared, but, as none of them have dealt in a detailed manner with the subject of this paper, it is unnecessary to enumerate them here.¹

The most obvious peculiarities in the anatomy of this animal are those which have relation to the immense development and singular displacement of the anterior limbs, and it is to the discussion of these that I propose to devote the present paper; the forearm has already been treated at some length in the pages of this *Journal* by Mr D'Arcy W. Thompson (vol. xviii. p. 406), and I shall therefore confine my remarks to the proximal portion of the limb.

Following the usual order of anatomical description we first proceed to the consideration of the bones.

Osteology.—The shoulder-girdle of the adult mole is composed of two bones, the scapula and the so-called clavicle.

¹ In Mr Dobson's beautiful *Monograph of the Insectivora* a very excellent description is given of the nearly related form *Condylura cristata*, together with some notes upon *Talpa europæa*.

The Scapula.—This is extremely narrow, and somewhat prismatic in shape, its vertebral border being only one-sixth of the length of the axillary border; the mesoscapular spine, at no part prominent, is in its middle third almost obliterated; at its vertebral extremity a blunt, somewhat conical process (*a*) (fig. 1) is produced, the principal purpose of which appears to be to afford a surface for the attachment of the posterior division of the trapezius. At its glenoid extremity the spine expands into a broad and thick, but stunted acromion (*b*), at the extremity of which may be seen two well marked facets for the strong acromio clavicular ligament and acromial portion of the subclavius respectively.

The supraspinous fossa, in the glenoid half of the bone, appears merely as a shallow groove on the anterior surface of the acromion, but in the vertebral half (*c*) it is of fair extent. The infraspinous fossa, of much less extent than the preceding, is almost absent in the middle third of the bone, being continuous with and almost indistinguishable from the axillary border. It exists as a broad but shallow groove behind the acromion; and at its vertebral extremity it forms a deep fissure (*d*) which is overhung by the spine.

The axillary border presents near the angle a large triangular somewhat rough surface limited internally by a sharp ridge; the surface affords origin to the large and powerful *teres major*.

At the glenoid extremity of this border is a wide concave surface, on the inner or vertebral margin of which is a small tubercle (fig. 2, *a*) supporting a facet for the origin of the *biceps*. The outer or dorsal margin of this surface is formed by a slight ridge which, proceeding upwards, crosses obliquely the infraspinous fossa and intersects the spine about its middle. This ridge limits anteriorly the extensive origin of the long head of the *triceps*, which occupies the whole of the surface above described.

The anterior border at its glenoid extremity is almost indistinguishable from the supraspinous fossa with which it blends, but above it is thin and sharp excepting near the angle, where it widens out to form a somewhat oval concave surface for the insertion of the *levator anguli scapulæ*.

The vertebral or suprascapular border is, in its anterior two-thirds, comparatively thin, and bears on its ventral aspect two

small facets, the more anterior (fig. 2, *b*) of which, narrow and elongated, gives attachment to the anterior trapezius, whilst the posterior (fig. 2, *c*), which is oval and concave, marks the insertion of the serratus magnus.

In its posterior third the vertebral border widens out greatly, forming a wide surface which affords attachment to the teres major, posterior trapezius, serratus magnus, and rhomboideus.

The subscapular fossa is as such confined to the vertebral half of the bone, the ventral aspect of the glenoid half being occupied by a prominent ridge; this ridge (fig. 2, *d*) supports the bicipital impression and extends to the margin of the glenoid cavity.

The glenoid cavity is elongated and deeply concave, its long diameter being placed obliquely to the vertical plane of the bone, an arrangement which is rendered necessary by the position in which the humerus is carried. There is a small facet on what would be, if the glenoid cavity had its usual direction, the anterior margin; this marks the scapular attachment of the glenohumeral ligament. There is no coracoid process, a fact which is sufficiently explained by the composite nature which Professor Parker ascribes to the so-called clavicle.

The clavicle, or more properly speaking the *coraco-clavicle*, is a curious irregular little bone which articulates with the humerus and the presternum but not with the scapula.

On its outer aspect is an oval or saddle-shaped surface (fig. 3, *a*) for articulation with a corresponding surface on the humerus, and its inner aspect is occupied by a narrower concave, somewhat reniform surface (fig. 4, *a*) for articulation with the presternum.

The anterior surface is deeply concave from side to side but convex vertically, especially at its upper part, where it turns over and merges into the posterior surface. The sides of the concavity are produced into ridges which afford attachment to muscles and the external ridge widens out below into a triangular surface (fig. 4, *b*) which gives origin to a portion of the deltoid. The posterior surface is limited above by an obliquely transverse, rounded ridge produced by the folding over, so to speak, of the superior margin; below this is a concave surface of quadrilateral form (fig. 3, *b*), in which some fibres of pectoralis minor are inserted.

The ventral surface is mainly occupied by a prominent obliquely truncated conical process (figs. 3 and 4, *c*), which is directed ventrally and inwards; on its inner aspect, near the free extremity, is a rough surface which gives attachment to the pectoralis minor, and at its base, at the junction of the anterior and ventral surfaces, is a minute foramen (fig 4, *d*), which Professor Parker believes to represent the coracoid fenestra.

The Sternum.—*The manubrium* is of very large size and greatly produced anteriorly, its length being nearly equal to that of the mesosternum and xiphisternum together. It is considerably expanded, especially at its middle part, and on its ventral aspect is produced a very prominent ridge or keel, which when viewed in profile is seen to have somewhat the form of the lateral half of a coffin lid. The free edge of that portion of the keel which lies behind the angle or promontory is thin and sharp, excepting where it widens out to form part of the articular surface for the mesosternum; in front of the promontory the edge is thick and rounded and expands anteriorly to support the articular surfaces for the coraco-clavicles. The promontory itself supports a tubercle which gives origin to a portion of the pectoralis major.

The anterior surface, which looks somewhat dorsally, is triangular in shape, the apex pointing upwards and backwards; it is convex both from side to side and from above downwards, and is traversed by a median longitudinal ridge. The convex surfaces on either side of this ridge form the articular surfaces for the coraco-clavicles, and the ridge itself gives attachment to some of the fibres of the anterior sternoclavicular ligament.

Viewed from the dorsal aspect the manubrium is seen to be produced laterally into a pair of somewhat triangular alæ (fig. 6, *a*) behind which the bone is rather narrow; at the posterior end is a thickened mass (*b*) which carries the surface for articulation with the mesosternum.

The space between the alæ (that is, the anterior three-fifths of the dorsal surface) is occupied by a deep groove (*c*), which, commencing anteriorly in the middle line, deviates considerably, as it proceeds backwards, to the right side. In the floor of this groove, at about its middle, is a small foramen (*d*), which pierces the root of the left ala.

The first rib articulates with the presternum, but there is no discernible facet for its reception.

The mesosternum consists of four pieces, of which the two posterior are, in the adult, immovably ankylosed.

The xiphisternum is narrow and pointed, and supports at its extremity a broad leaf-like cartilaginous expansion.

The sternum is directly connected with eight ribs, of which the two posterior unite at their sternal ends and together are received into the space between the meso- and xiphisternum.

The Humerus.—This bone is extremely short, broad, and flattened, and the muscular impressions on it are mostly very pronounced.

The upper part of the anterior¹ surface is occupied by a large concave rhomboidal surface (fig 7, *a*), which marks the insertion of the deltoid. At its lower angle is a rough triangular surface (fig. 7, *b*) for the insertion of a part of the complex pectoralis major, and at its inner angle is a deep notch (*c*) continued downwards for a short distance into a shallow groove (*d*); this is the lower portion of the bicipital groove.

The upper external border of this space is formed by a slight groove which separates it from a broad, smooth, convex surface which articulates with the coraco-clavicle.

Below the bicipital notch is a very prominent outstanding process (fig. 7, *e*) bearing two distinct impressions, for the *teres major* and *latissimus dorsi* respectively.

At the base of the internal condyle is a deep circular pit (*f*) which gives origin to the powerful ligamentous flexor sublimis digitorum; the pronator ridge is thin, sharp and very prominent, and is produced above into a pointed process (*g*). There is a large supra-condylar canal, the lower opening of which (*h*) is on the anterior aspect of the bone.

The external condyle is drawn out into a styloid process (*i*) of considerable length, which points upwards and slightly outwards, and at its base is seen the almost hemispherical capitellum (*j*). At the summit of the bone is the superior opening of the bicipital canal (*k*).

¹ For the sake of convenience in description the bone is supposed to be placed as in the figures, although this is by no means its natural position in the animal (see movements of the limb).

Turning now to the posterior aspect of the bone we notice that the head (fig. 8, *a*) is very prominent and vertically elongated, that it looks directly backward, and that it is not placed at the superior extremity of the bone, but that, projecting considerably above it on its inner side, is a ridge (fig. 8, *b*) which represents the inner tuberosity.

External to the head is the smooth articular surface for the coraco-clavicle (fig. 7, *l*, and fig. 8, *c*), upon which and close to the head is a small, shallow depression which marks the insertion of the supraspinatus; this surface is limited inferiorly by a jagged irregular ridge (*d*), at the outer end of which is a hook-like process (*e*) bearing a facet for the infraspinatus. The articular surface above described represents the outer tuberosity.

Close to the outer side of the head is a shallow groove which lodges the gleno-humeral ligament, and internal to the head is a deeper groove for the attachment of a thickened band of the capsular ligament.

Internal to and somewhat above the head is a ridge (*f*) which overhangs the bicipital groove, and upon which is an impression for a part of the pectoralis major.

The bicipital groove is very curiously modified, being, in its upper part, converted into a complete bony canal which commences at the summit of the bone (*g*), and passing downwards and inwards for about $\frac{1}{8}$ in. opens out into a groove (fig. 8, *h*) which terminates at the notch before spoken of.

Another very curious condition, which occurs in the upper part of the bone, is a large cavity (*i*), somewhat similar to that found in the humeri of birds. This cavity is conical in shape and excavates the upper portion of the bone so extensively as to convert it into a mere shell, the walls of which are comparatively thin and in some places quite translucent.

The inner tuberosity bears two very distinct facets, which mark the insertions of the subscapularis.

The olecranon fossa is very deep, but there is no intercondylar foramen; at the apex of the fossa is a foramen (*j*) large enough to admit a very coarse bristle (in some bones there are two somewhat smaller ones), which opens directly into the medullary cavity.

The trochlear surface (*k*) is placed mainly upon the posterior aspect of the bone.

Ligaments.—If Professor Parker's views concerning the nature of the bone usually called clavicle be correct, we must regard the articulation between that bone and the humerus as part of the true shoulder-joint. It is, however to be observed that there are two separate synovial cavities, that the articular surfaces on the humerus are not continuous, and that the cavities of the joints are separated by ligamentous partitions.

The ligaments of the scapulo-humeral articulation are—(1) Capsular, and (2) Gleno-humeral.

1. *The Capsular ligament* presents nothing worthy of remark with the exception of a thickening of its substance on the inner side of the joint.

2. *The Gleno-humeral ligament* is a stout, cord-like structure which passes from a small facet above the glenoid cavity to a small, shallow depression at the lower and posterior portion of the articular surface for the coraco-clavicle close to the head.

In its course it lies within the capsule and is separated from the cavity of the joint by the synovial membrane only.

In addition to these structures the tendons of the supraspinatus and biceps exercise ligamentous functions.

The tendon of the supraspinatus is broad and thick and is inserted into a small impression between the articular surfaces for the scapula and coraco-clavicle; it thus, becoming intimately adherent to the capsules of both joints, forms a strong partition between them.

The influence of the tendon of the biceps upon the movements of the limb is fully discussed in the section of this paper which is devoted to the actions of the muscles, but it may be here stated that when the muscle is at rest the tendon will probably function as a ligament, steadying the humerus, holding it in apposition with the scapula and limiting its external rotation.

The claviculo-humeral joint possesses a *capsular ligament*, the anterior portion of which becomes considerably thickened, being converted into a broad sheet of strong vertical fibres, which are inserted into a groove at the anterior margin of the articular surface on the humerus.

The acromio-clavicular ligament.—This very thick and strong band of fibres proceeds from the anterior of the two facets

on the acromion to a small flat surface on the posterior margin of the outer surface of the coraco-clavicle. At about its middle it receives the insertion of a part of the subclavius.

The sterno-clavicular articulation.—The coraco-clavicle is bound to the presternum by two ligaments, one of which, placed on the anterior and dorsal aspect of the joint, is of considerable strength. Its fibres, which arise from the anterior margin of the internal surface of the coraco-clavicle, proceed, some of them to the head of the presternum, others to the bone of the opposite side. It therefore agrees closely with the interclavicular ligament of human anatomy.

The posterior sterno-clavicular ligament is a comparatively thin sheet of fibres which extends from the posterior margin of the articular surface of the coraco-clavicle to the corresponding margin of the articular surface of the presternum. There is no interarticular fibro-cartilage in this joint, but that structure is probably represented by the plate of cartilage which covers the articular surface of the coraco-clavicle, this being what remains of the so-called "fourth coracoid segment" of Parker, who regards it as constituting with its fellow "the moieties of a highly modified omosternum."¹

The interscapular ligament.—This unique and extremely interesting structure consists of a thick tendinous cord passing from the base of one scapula to that of the other, its attachment being nearly opposite to the spine: it is continuous anteriorly with the ligamentum nuchæ; and some of the muscles which arise from that structure, as *e.g.*, splenius, have also an origin from it. From its posterior surface in the middle line, a band of connective tissue passes backwards to the spine of the third or fourth dorsal vertebra, and appears to be a backward continuation of the nuchal ligament. The interscapular ligament affords attachment to several muscles—trapezius, teres major, serratus posticus superior and dorso-interscapularis, some of which it appears to have considerably modified.

It becomes a matter of some difficulty to determine what is the nature of this ligament, for, that it represents some structure which exists in other animals there can be little doubt. Some light seems to be thrown upon the subject by the following facts:

¹ Monograph on the Shoulder-girdle and Sternum, Ray Soc., 1868.

—(a) the vertebral spines are almost completely absent from the third cervical to the tenth dorsal; (b) the interscapular ligament is in intimate relation with the ligamentum nuchæ, as well as with some of the muscles which arise from it; (c) an ossification has long been known to exist in the latter structure in the cervical region; (d) certain muscles are profoundly modified by their relation to the interscapular ligament.

These facts appear to bear upon the subject in the following manner: the abortion of the dorsal spines explains the existence of the ligamentum nuchæ, or rather its backward continuation, in the dorsal region, and the intimate relation of the ligamentum nuchæ, with the interscapular ligament, implicates the latter in the changes which have occurred. The abortion of the vertebral spines, together with the ossification in the nuchal ligament, seems to indicate that the latter structure may possibly consist, not merely of separated interspinous ligament, but also of the detached spinous elements of some of the vertebræ, and this conjecture is rendered more probable by the circumstance that the so-called “nuchal style” commences abruptly immediately behind the prominent spine of the axis. The most important of the muscular modifications above referred to occurs in connection with the serratus posticus superior. This muscle arises from the anterior surface of the interscapular ligament and proceeds to its usual insertion, whilst, arising from the rudimentary spines of the fourth and fifth dorsal vertebræ, and from the backward prolongation of the ligamentum nuchæ is a small triangular muscle, which I have called dorso-interscapularis,¹ which is inserted into the outer two-thirds of the posterior surface of the interscapular ligament, and which is separated from its fellow near its insertion by a small triangular interspace which is filled by the ligamentum nuchæ.

If it be assumed that the interscapular ligament has been produced by the metamorphosis of the spinous elements of some of the vertebræ, or by an outgrowth of the ligamentum nuchæ, it would seem that the region in which the changes have occurred corresponds with the origin of the serratus posticus superior, and

¹ This muscle is called rhomboideus posticus by Dr Dobson, whose views concerning its morphological nature are somewhat different from those above given. *Vide A Monograph of the Insectivora*, part ii.

that the mass of changed tissue, extending outwards through the substance of the muscle, has cut off, so to speak, its postero-internal angle, which has persisted as a separate muscle in the position which it now occupies.

MYOLOGY.—The muscles of the anterior limb are, as would be anticipated, extremely well developed, and present several interesting deviations from the conditions most commonly found in mammals.

We shall first consider the muscles which pass from the trunk to the limb and limb girdle.

Pectoralis Major.—This muscle is not only of very large size, but is split up into a number of remarkably distinct fasciculi which may be conveniently distinguished by attaching numbers to them.

The posterior superficial mass (P.M. 1, fig. 9) is of large size, and evidently corresponds with the sternal portion of human anatomy; it arises the whole length of the sternum, behind the promontory of the manubrium, including the expanded xiphoid cartilage and from all the sternal ribs. From this origin its fibres converge towards the crest (fig. 8, *b.*) above the bicipital groove, where they are inserted without having become tendinous. As it approaches its insertion, however, this portion of the muscle becomes covered with a layer of glistening tendinous fibres. At its anterior border is placed a flattish, fusiform fasciculus (P.M. 2, fig. 9), which arises from the promontory of the presternum, and is inserted into the same portion of the humerus. Anterior to this, and separated from it by a small interspace, is a narrow fasciculus (P.M. 3) arising from the head of the manubrium and passing outwards to be inserted into the angle above the bicipital notch. In front of this is a somewhat large quadrilateral piece (P.M. 4), which has no sternal or costal origin but arises from a median sheet of connective tissue which is interposed between it and its fellow of the opposite side.¹ It is inserted into the whole length of the outer bicipital ridge and into the triangular surface at the lower angle of the rhomboidal

¹ This condition of the pectoral muscles is of considerable interest in connection with the opinion expressed by Miss Lindsay in a paper read at the Zoological Society on June 16, 1885, that the sternal keel of carinate birds "is an outgrowth of the sternum of comparatively late phylogenetic date, and created for and by the attachment of the pectoral muscles."

space. The two muscles, when in action, must pull against one another, since they have no central bony attachment. They are probably homologous with the "clavicular portion" of human anatomy.

Upon reflecting the sternal portion of the muscle (P. 1) there is seen, underlying it, a very distinct fasciculus (P. 5) which arises from the posterior three-fourths of the crest of the manubrium and from the second rib. It is inserted into the posterior surface of the inner tuberosity, becoming covered, as it approaches its insertion, with a layer of tendinous fibres. Behind this is a somewhat larger mass (P. 6), which arises from the second and third sternal ribs and blends more or less with the first part (P. 1) at its insertion. A seventh fasciculus, small and narrow (P. 7), takes origin from the promontory of the presternum and is inserted into the angle above the bicipital notch a little above the insertion of the third fasciculus. *Pectoralis minor* is of medium size and arises from the anterior half of the keel of the presternum and by a small tendinous slip from the first sternal rib. It is inserted into the ventral surface of the coraco-clavicle.

Subclavius.—This muscle, which is of large size, arises from the whole length of the dorsal surface of the presternum on either side of the median groove, as well as from the greater part of the anterior surface of the first rib; it fills up to a great extent the large space which intervenes between the first rib and the coraco-clavicle. Arriving at the anterior portion of this space, the muscle separates into two parts, each of which ends in a tendon. The more internal of these divisions proceeds to the outer third of the dorsal margin of the coraco-clavicle as well as to the adjacent part of the anterior surface, whilst the more internal of the two is inserted into the anterior surface of the short acromion and into the acromio-clavicular ligament.

Trapezius.—This consists of two thin and slender muscles which are entirely separate both in their origin and insertions; the anterior arises from the outer two-thirds of the superior curved line of the occipital bone and is inserted into the dorsal lip of the vertebral border of the scapula in the supraspinous region. It lies at the side of the neck, separated from its fellow by the rhomboid, which overlaps it at its posterior end. The

posterior segment, which is a thin ligulate muscle, arises from the last dorsal and all the lumbar spines, by tendinous fibres, and is inserted into the conical process on the spine of the scapula. In close relation, externally, with this portion of the trapezius is a very thin and narrow ribbon of muscle, the dorso-orbicularis, which passes forwards to be inserted into the skin of the dorsal region just behind the posterior border of the orbicularis panniculi.

Rhomboideus.—There is only one rhomboid muscle, and this is probably the representative of rhomboideus minor of man. It is a somewhat large muscle, arising from the ligamentum nuchæ and from the curious little styloform bone which exists in this region. From this origin it passes backwards and outwards, and becoming somewhat twisted upon itself, is inserted into the vertebral border of the scapula in the supraspinous region.

In the posterior part of its course it lies superficial to the trapezius, a circumstance which is due to the entire absence of the central portion of the latter muscle and the abnormal position of the scapula, to which allusion has been already made.

Latissimus dorsi is of rather large size and consists of two portions, which are separated by a cellular interspace. The anterior portion, which is the smaller, arises from the lower five dorsal and first lumbar spines, and passing forwards soon comes to lie under cover of the posterior portion, with which it blends near its insertion. The posterior portion arises from the remaining lumbar spines, from the lumbar fascia, and from the fascia covering the external oblique; it is aponeurotic at its origin, but soon becomes fleshy, at the same time becoming rapidly narrower, as it winds round the thorax to reach the axilla. It terminates in a broad flat tendon, which unites to a great extent with that of teres major, and the united tendons are inserted into the prominent ridge below the bicipital groove. Although the tendons are almost entirely blended the facets on the bone for their insertion are quite distinct, the more anterior belonging to latissimus dorsi.

Serratus magnus arises by seven fleshy digitations from seven ribs,—the second to the eighth—near their angles, and is inserted into the oval facet on the ventral lip of the vertebral border of

the scapula, the posterior part of the border and the interscapular ligament.

Levator anguli scapulæ, which is nearly as large as the serratus magnus, from which it is separated by a cellular interspace, arises from the transverse processes of the cervical vertebræ from the third to the seventh inclusive, and is inserted into the oval surface at the vertebral end of the anterior border of the scapula.

As the serratus posticus superior has, in the mole, an attachment to the shoulder girdle, it may, together with its concomitant, the dorso-interscapularis, be properly described here.

Serratus posticus superior is a small narrow muscle which arises from the central portion of the ventral aspect of the interscapular ligament, and passes outwards to be inserted by two digitations into the third and fourth ribs near their vertebral ends.

Dorso-interscapularis, the nature of which has been fully discussed under the heading of ligaments, is a small triangular muscle which arises from the spines of the fourth and fifth dorsal vertebræ, and from the backward prolongation of the ligamentum nuchæ, and is inserted into the outer two-thirds of the posterior surface of the interscapular ligament.

We now proceed to consider the muscles which pass from the shoulder girdle to the brachium.

Deltoid.—This is of comparatively small size, and owing to this fact, to the large size of the great pectoral, and particularly to the singular position of the limb, lies entirely under cover of the quadrilateral fasciculus of the pectoralis major; it arises from the outer half of the anterior surface of the coraco-clavicle, and is inserted by fleshy fibres into the whole of the rhomboidal space on the front of the humerus and by tendinous fibres at its margins. It is thus seen that the deltoid has no scapular attachment.

Teres major.—This muscle is of enormous proportions, being perhaps more hypertrophied than any of the arm muscles; it arises from the triangular rough surface at the posterior angle of the scapula, from the upper two-thirds of the axillary border, from the broad surface on the vertebral border by tendinous fibres, by a small additional slip from the anterior portion of the vertebral border and, lastly, from the interscapular ligament. From this somewhat complicated origin, its fibres pass forwards,

forming a large fleshy belly, which tends to become more or less blended with surrounding muscles, and terminate in a strong, flat tendon, which unites largely with that of latissimus dorsi, and is with that tendon inserted into the ridge below the bicipital groove, the moiety of the tendon which belongs to teres major being inserted into the posterior of the two facets.

Subscapularis is a somewhat small muscle, compared with the great teres major; it arises, as usual, from the whole of the subscapular fossa, as well as from the ridge on the ventral surface of the neck. The substance of the muscle is penetrated by two tendons upon which the fibres are, so to speak, gathered up, and which are inserted into two round concave facets at the summit of the inner tuberosity, immediately internal to the superior opening of the bicipital canal. Into the surface of bone which intervenes between the two facets, the muscle has a fleshy insertion.

Supraspinatus is a somewhat small penniform muscle, which arises from the whole of the supraspinous fossa up to the margin of the glenoid cavity; its fibres converge upon a strong flat tendon, the size of which is, in relation to the muscle to which it belongs, somewhat disproportionately large, which, uniting to some extent with, and piercing, the capsule of the claviculo-humeral joint is inserted upon the surface of the humerus which articulates with the coraco-clavicle, lying in the cavity of the joint, and covered with the synovial membrane.

This tendon also becomes adherent to the capsule of the true shoulder joint, forming, as already stated, a partition between that joint and the claviculo-humeral articulation.

Infra-spinatus, of small size arises from the greater part of the infraspinous fossa, and also from the truncated, conical process at the vertebral end of the spine. It is inserted by a small tendon into a facet at the base of the uncinat process on the outer tuberosity of the humerus.

Teres minor appears to be entirely absent. We now pass on to the consideration of those muscles which extend from the shoulder girdle to the forearm.

Biceps brachii.—This muscle is perhaps more remarkably modified than any other in this region; it arises by a thin cord-like tendon from a small tubercle on the ventral surface of the

scapula about $\frac{1}{16}$ of an inch from the margin of the glenoid cavity; from this point the tendon passes forward and downward to reach the superior opening of the bicipital canal. The axis of this canal being as nearly as possible at right angles with the portion of tendon intervening between it and the scapula, the tendon becomes bent up, playing over a small trochlear surface at the posterior edge of the superior opening. Emerging from the canal, but lying in the deep bicipital groove, the tendon follows the same course until it reaches the bicipital notch on the inner side of the humerus, where it again changes its course, twisting sharply round the polished pulley-like margin of the bone and coming now to have a direction at right angles to the last. It now swells out into a fleshy belly of considerable size, and this becomes contracted into a strong flat tendon which is inserted in its normal position on the radius. It is thus seen that the tendon of the biceps lies in three different planes, each forming a right angle with either of the others.

Triceps is of large size and has the following characters:—A large quadrilateral mass divided into two portions by a cellular interspace arises from the rough surface at the glenoid end of the axillary border of the scapula, and from the infraspinous fossa for about $\frac{2}{3}$ of the length of the bone; another distinct mass arises from the posterior surface of the humerus below the bicipital groove, and a third arises from the outer and posterior surface of the humerus and from the conical cavity at its upper part. The muscle is inserted, mainly by fleshy fibres, into the enormous expansion of the olecranon.

Brachialis anticus arises from the upper portion of the outer surface of the humerus below the rhomboidal space, and from the hooklike process on the outer tuberosity; its strong, flat tendon is inserted into a small depression in front of the coronoid process of the ulna.

Anconeus.—This muscle consists of two parts separated by a small cellular interspace; the posterior portion is a round fusiform fasciculus arising from the tip of the styloid external condyle and inserted into the outer projection of the olecranon. The anterior portion, thin and fan-shaped, arises in common with the preceding and becoming somewhat aponeurotic as it passes

over the extensor muscles of the forearm, is inserted into the prominent crest of the ulna.

Epitrochleo-anconeus or *anconeus internus*, a comparatively large muscle of a triangular shape, arises from the posterior surface of the pronator ridge, and passing almost horizontally backwards, is inserted into a prominent process on the inner side of the olecranon. It lies superficial to the ulnar nerve.

The present paper would be incomplete without a brief notice of the parts which are played in the economy of the mole by the numerous and important modifications of anatomical structure which have been described. The movements of which the pectoral limb of the mole is capable, present extremely little variety, being almost entirely confined to a backward and forward movement like the oar of a boat or the arm of a swimmer, which latter it closely resembles, and consisting, like it, of a "stroke" in which the outspread hand is driven forcibly through a more or less dense and resisting medium, and a "recovery" in which comparatively little resistance has to be overcome and therefore comparatively little force used.

To the execution of the former of these movements the limb is specially adapted, and it is to the hypertrophy of the muscles by whose agency it is performed, that the structural modifications are mainly due. This will be seen more clearly if we examine the movements in detail, and observe the manner in which the several muscles contribute to their production. Thus upon analyzing the first movement, the backward "stroke" of limb, we find that it is made up of the following parts: (a) flexion of the humerus upon the scapula; (b) extension of the forearm; (c) rotation of the humerus around its longitudinal axis, and as a result of this; (d) flexion of the digits.

(a) Flexion of the humerus upon the scapula is mainly effected by the long head of the Triceps, which, by virtue of its very extensive attachment to the scapula and the great development of the olecranon, acts at a great mechanical advantage, and its action is probably largely supplemented by the infraspinatus as well as by the teres major and the latissimus dorsi.

(b) The principal action, however, of the two latter muscles is that of rotation of the humerus around its long axis, in which

action they are powerfully assisted by the posterior segment of the great pectoral.

This movement is of a twofold character, consisting of (1) a rotation of the humerus around a line drawn through the middle of the trochlear surface and the scapular head, and (2) a backward movement of the entire bone, carrying with it the scapula, upon the coraco-clavicle. The latter movement is obviously brought about entirely by the pectoralis major and latissimus dorsi, whilst the former is in a great measure due to the teres major.

(c) The rotation of the humerus results in flexion of the digits in the manner described by Mr D'Arcy W. Thompson in his admirable paper on the subject (*Journal of Anatomy*, vol. xxiii. p. 406).

The teres major and latissimus dorsi have been above described as rotating the humerus outwards; it must be borne in mind that as this bone is inverted, these muscles come to lie on the outer aspect of the limb, a circumstance which, no doubt, led Professor Owen into the error of confounding the teres major with the deltoid.¹

(d) Extension of the forearm is of course effected by the action of the triceps.

In the forward movement of the limb the resistance to be overcome is very much less, whence the muscles which are called into action are of less robust proportions. The movement is, of course, merely a reversal of the preceding, viz., extension of the humerus upon the scapula; flexion of the forearm; internal rotation of the humerus and extension of the digits. Extension of the humerus upon the scapula is effected chiefly by the anterior segment of the great pectoral, the deltoid and the supraspinatus, which muscles, assisted by the biceps, as explained below, rotate the humerus inwards. The digits are extended by the strong extensor communis and the elbow is flexed by the brachialis anticus and biceps, the latter functioning also as a rotator of the humerus in a very curious and interesting manner. It has been pointed out (p. 215) that the long proximal tendon of

¹ "The deltoid, coextensive with the scapula, acts through its length with great power upon the well-developed humeral ridge."—*Anatomy of Vertebrates*, vol. iii. pp. 17, 18.

this muscle runs a zigzag course somewhat like a capital Z, and that the middle portion lies in a bony canal in the upper part of the humerus, the canal passing almost horizontally through the bone in its transverse diameter.

From this it clearly follows that when, by the contraction of the muscle, the tendon is put upon the stretch, it will tend to become straight, and the result of this will be an external (or in the inverted position of the humerus an internal) rotation of the bone and consequent relaxation of the flexor sublimis ligament permitting of extension of the digits.

Thus it will be seen that the singular condition of the biceps comes to be of material use in the curiously modified muscular movements.

EXPLANATION OF PLATE V

Fig. 1. Left scapula, dorsal aspect. *a*, mammillary process at vertebral end of spine; *b*, acromion; *c*, supra-spinous fossa; *d*, infra-spinous fossa.

Fig. 2. Left scapula, ventral aspect. *a*, bicipital impression; *b*, facet for trapezius; *c*, facet for serratus magnus; *d*, ventral ridge.

Fig. 3. Left coraco-clavicle, posterior aspect. *a*, articular surface for humerus; *b*, posterior surface; *c*, conical process on ventral surface.

Fig. 4. Left coraco-clavicle, anterior aspect. *a*, articular surface for presternum; *b*, surface for deltoid; *c*, conoid process; *d*, foramen (coracoid foramen, Parker.)

Fig. 5. Presternum and coraco-clavicles, ventral aspect. *a*, alar expansion; *b*, thickening at posterior extremity; *c*, carina; *d*, promontory.

Fig. 6. Presternum and coraco-clavicles, dorsal aspect. *a*, ala; *b*, posterior end; *c*, groove; *d*, foramen.

Fig. 7. Left humerus, anterior aspect. *a*, rhomboidal space occupied by deltoid; *b*, surface for part of great pectoral; *c*, bicipital notch; *d*, termination of bicipital groove; *e*, ridge for teres major and latissimus dorsi; *f*, pit marking origin of flexor sublimis digitorum; *g*, pronator ridge; *h*, lower opening of supra-condylar canal; *i*, external condyle; *j*, capitellum; *k*, superior opening of bicipital canal; *l*, articular surface for coraco-clavicle.

Fig. 8. Left humerus, posterior aspect. *a*, head; *b*, inner tuberosity; *c*, outer tuberosity (articular surface for coraco-clavicle); *d*, ridge on tuberosity; *e*, uncinatè process; *f*, ridge for part of great pectoral; *g*, superior opening of bicipital canal; *h*, bicipital groove leading down

to bicipital notch; *i*, cavity in outer tuberosity; *j*, nutrient foramen; *k*, trochlear surface.

Fig. 9. Dissection of the muscles of the pectoral and axillary regions. On the right side the superficial, on the left the deep muscles are shown. P.M. 1-5, pectoralis major; the sixth and seventh fasciculi have been removed, the former in order to show the subscapularis, and the latter to show the pectoralis minor. P.Mi., pectoralis minor; S, subscapularis; T.M., teres major; Bi., biceps; P.R.T., pronator radii teres; F.C.R., flexor carpi radialis; D., deltoid; E.O., external oblique; F.S.D., flexor sublimis digitorum (converted into a ligament); E.C.D., extensor communis digitorum; Ra., radius.

Fig. 10. Dissection of the brachium and fore-arm from the inner side. Sc., Scapula (the axillary border and subscapular fossa shown). Tr. 1., scapular head of biceps; Tr. 2, outer head; Tr. 3, inner head; C.L. capsular ligament; Bi. 1, tendon of biceps above bicipital canal. Bi. 2, tendon of biceps emerging from canal; Bi. 3, belly of biceps; I.T., inner tuberosity; A.I., anconeus internus; P.R.T., pronator radii teres; F.C.R., flexor carpi radialis; P.L., palmaris longus; F.C.U., flexor carpi ulnaris, F.S.D., flexor sublimus digitorum.

ON THE REPRODUCTION OF THE CARAPAX IN
TORTOISES. By HANS GADOW, Ph.D., M.A. *Cantab.*,
Strickland Curator and Lecturer on Advanced Morphology
of Vertebrates, University, Cambridge. (PLATE VI.)

AMONGST a number of land tortoises (*Testudo graeca*) kept here were many specimens which, owing to the rough mode of packing generally gone through by these hardy reptiles, arrived in a very injured condition. In some cases the greater part of the carapax was broken through, most of the plates having been so much cracked or crushed that they were dislodged from their neighbouring parts, and were rendered easily movable. This refers not only to the epidermal scutes, the so-called tortoise-shell, but likewise to the underlying ossified dermal plates.

All the tortoises have since been kept under the most favourable natural conditions, whereupon the maimed specimens showed the following interesting changes:—

The epidermal scutes fell off, followed, after some three to ten months, by the thick osseous plates, which were completely atrophied and then raised above the old surface, until the greater portion of the old carapax was bodily lifted up and was kept in connexion with the animal merely by the overlapping margins of some of the neighbouring uninjured scutes. Underneath this old armour, and separated from it by a space partly filled with decaying matter, comes a layer of new tortoise-shell. This layer is of typical structure, and even contains the usual patches of black and yellow pigment. In bad cases the whole renewed area is covered with a mass of horny large tubercles without any regular arrangement. Underneath this shell comes a soft, vascular, and apparently sensitive layer, resembling the malpighian normally found between the tortoise-shell and the ossified cutis. Underneath this soft layer lies a more or less well ossified armour. In one of the most injured specimens about four neural and six costal plates of the dermal armour were bodily lifted off (fig. 1). The animal was then protected only by the remaining subcutaneous connective tissue, which although already considerably changed and thickened, was still so soft

that it was bulging in and out according to the expiration and inspiration of the lungs. On this soft cover there was already produced some irregular and imperfect tortoise-shell. Microscopic examination in transverse stained sections shows the following structure (fig. 2A):—*s.c.*, stratum corneum, partly peeling off; the lower layers are composed of more flattened cornified cells, followed by high cylindrical cells (M), which, like the typical malpighian cells of Chelonians, show granulous contents with a large nucleus and nucleolus; *P*, black, star-shaped pigment clusters; *o.c.*, ossified cutis, *i.e.*, new dermal armour. Sections through less advanced portions show the thick cutis (fig. 2B, *c*) composed of the normal horizontal connective fibres and full of osteoblasts. Towards the peritoneal or inner side these are by far less numerous and the fibres are still irregularly felted, as in ordinary subcutaneous connective tissue.

In another case the epiplastron had been severed from the neighbouring entoplastral and hyoplastral plates. The opposite margins are now quite smoothly rounded off, and the epiplastron is now connected with the rest of the plastron by a belt of skin of 0·5 cm. in width, consequently quite movable, but of course attached to the skin of the neck and the *M. claviculo-plastro-humeralis*. When this animal withdraws its head into the shell, the new jointed epiplastron shuts part of the opening and thus bears a close resemblance to the mechanism of the genus *Pyxis*. The belt of skin cannot in its structure be distinguished from that of the neck and legs.

In order to investigate this process, I made the following experiments on *Testudo græca*. The specimens are now in the museum of comparative anatomy and zoology in Cambridge. In November 1884 a ring of three-quarters of an inch in diameter was cut through the whole carapax into the soft subcutaneous tissue. The central disk, which had thus become a movable plug, remained intact. The walls of the ring and disk were cauterised in order to destroy the margins of the malpighian layer. The wound was for the first fortnight dressed antiseptically, but afterwards left to itself. The plug showed the inspiration and expiration for several weeks, and remained movable for at least three months. Now, in September 1885, examination shows the following result (fig. 3):—

The walls of the ring R looked as if the wound had not been mended, but after slight pressure a ring of necrotic dermal bone, D, came off and showed the continuation of the malpighian layer M. Dead tortoise-shell, together with a disk of dermal armour could easily be removed from the top of the disk. The dermal part D was only half its original thickness, resorbed and necrotic on its deep surface. Below it, a layer of newly formed tortoise-shell, followed by malpighian stratum and then by dermal bone.

On another part of the tortoise a portion of the horny layer, together with the malpighian stratum, was completely removed to the extent of 0.3 inch square (fig. 4). This area reached across the natural suture of two neighbouring dermal plates. The injured place kept its appearance, apparently without change, for ten months. Now, with some force a thin layer of dermal plate could be removed; it was quite necrotic, and separated from the rest by a stratum of horny epiderm, which latter was continuous with the uninjured tortoise-shell. It must, however, be noted that this regenerated shell does not reproduce the peculiar pattern of concentric squares and rings visible on the uninjured scales, because this pattern is intimately connected with the growth of the whole animal.

To sum up, the injury done to the armour of tortoises is mended in this way that from the healthy margins of the malpighian layer the latter grows centripetally towards the injured area right into the osseous plate and thus causes the latter's partial destruction, whereupon the superimposed shell and osseous plates to the extent of the area to be mended are cast off. Lastly, the remaining deep portions of the dermis make up for the loss by thickening. If the injury is very severe, as in the tortoise figured, where the dermal armour was cast off down to the soft cutaneous layers, the bulk of these produces cutis, which then undergoes the normal process of ossification, until at last a new complete armour is formed.

A superficial centripetal growth of the epiderm over the defect, as in mammals, does not take place in tortoises. The reason for this rather roundabout process seems to be that the epidermal products (the tortoise-shell) are not only the phylogenetically older but also a more important protection than the much later

established dermal armour. However, we do not know of any non-pathological cases where bony or dermal structure lies superficially without being covered by epidermal products, with the single exception of the horns of deer, but these have to be periodically renewed.

Considering the enormous extent to which our tortoises have mended their shells, there may be after all some truth in the often ridiculed story related of Malayan turtle-fishers, who, after the living creature has been slightly roasted over a coalfire, to render the tortoise-shell easily removable, set the tortured turtle free so that it may recover and yield them a new coating.

I confess that at first sight the process of regeneration described above seemed to afford at last an instance of epidermal products being developed from the surface of cutaneous layers. One might suggest that through the development of the various skin-glands epiblastic elements had been conveyed deeply into the cutis and that these latent or dormant cells might under certain circumstances establish a malpighian layer. Such an assumption might, perhaps, hold in mammals, but Chelonians are, like most other reptiles, almost devoid of skin-glands. Or, if the mesoblast of the amniota is derived from both germinal layers, the upper portion of the mesoderm then being a descendant from, or perhaps a differentiation of, the ectoderm, we might assume, that the cutaneous layer retains in itself the potentiality for developing structures which normally are produced only by the ectoderm specialised in that direction. Such cases seem to occur. Professor Humphry kindly informs me that in cases of burns or other injuries, causing the destruction of large portions of the skin, the whole often considerable defect of epidermis and cutis will be mended by a regeneration from the cutis *per superficiem*, provided there be any of the deeper layers of the cutis left. An analogous case is the reproduction of bark from the whole surface of the cambium laid open after the destruction of the old cortex.

EXPLANATION OF PLATE VI

Fig. 1. Transverse section through carapax; *E.*, epiderm; *O.C.*, ossified cutis; *D.*, cast off portion of old dermal armour; *M.*, newly formed malpighian layer and new tortoise-shell; *x*, see fig. 2.

Fig. 2. Section through regenerated portion of carapax at point *x*, fig. 1. *A. s.c.*, stratum corneum; *M.*, cylindrical cells; *P.*, pigment clusters; *O.C.*, ossified cutis. *B. c.*, thick cutis.

Fig. 3. Transverse section; *R.*, the ring cut out; *D.*, cast off portion of dermal armour on disk; *D₁*, cast off portion of wall of ring; *O.C.*, ossified cutis or dermal armour, partly renewed at *r*; *E.*, cast off portion of old epiderm; *M.*, malpighian layer, newly formed.

Fig. 4. Transverse section; *D.*, cast off disk of dermal armour, below which the newly-formed tortoise-shell.

OBSERVATIONS ON THE DEVELOPMENT AND THE
DECAY OF THE PIGMENT LAYER ON BIRDS'
EGGS. By ALEXANDER M. M'ALDOWIE, M.D., *Vice-
President, North Staffordshire Naturalists' Field Club.*

MANY and various are the theories which have been brought forward by ornithologists to account for the coloration of birds' eggs, but all have failed to explain why the majority are so richly and beautifully ornamented. White eggs, deposited in dark situations, are accounted for, as also are those which simulate the colour of the soil or other material on which they are laid. All others, comprising by far the largest proportion of eggs, have proved an enigma as yet unsolved. Theorising on this interesting subject, it occurred to my mind that if we were to reverse the usual order of study, examine first the pigmentation of those eggs whose colours apparently bear no relation to their surroundings, and afterwards investigate the causes which might have brought about the loss of pigment in white eggs, and also the method by which protective mimicry had been produced, we might arrive at a more satisfactory and scientific conclusion. A review of other organic objects gave abundant reason for this order of investigation. White is one of the rarest hues in the organic world. When it occurs it is for some specific purpose, and its presence can always be easily accounted for. Thus, animals which live within the arctic circle are white like the snow of these regions, the perianth of many flowers is white to attract insects and ensure cross fertilisation, and most sea birds are white, with blue on the back, resembling the colours of the clouds, and rendering them less likely to frighten the fish upon which they prey.

Much has been written about the variety of colours observed on eggs, but a glance at the solar spectrum will at once show the fallacy of this opinion. The only portions of the spectrum represented on the whole range of colours of birds' eggs are a small band on the red (forty to forty-five), and another on the green (eighty-five to ninety-two).

This seems the more striking when we consider the number of

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colours exhibited by the birds themselves, where every part of the spectrum is represented, as well as by other organic objects, as insects, flowers, &c. Only two colours of pigment are found on eggs, green and red—together with black, which is not a colour in the scientific sense of the term. It is a remarkable fact, and one which I have never seen noticed by writers on the subject, that all the rich hues and shades with which eggs are so lavishly ornamented, are merely intermediates between these three.

I have arranged the following scale by an expansion of these three according to chromatic rules, and it will be seen that it embraces every shade of colour found in birds' eggs.

BLUE-GREEN	RUSSET or Orange Brown
Green	Brown
Olive-Green	Grey-Brown
Olive	Brown-Grey
Olive-Brown	BLACK or Grey.

The hæmatin of the red blood-corpuscles is the source of these pigments. It is taken up by the pigment cells where it undergoes metamorphosis into the green, brown, and black shades, and is then secreted by the particular follicles at the lower part of the uterus. "To understand how yellow, green, brown, and black pigments may be derived from the colouring matter of the blood," writes Rindfleisch, "we must first glance at the physiological metamorphoses to which this substance is liable. The most important of these, and in some sense typical of all the rest, is its transformation into bile-pigment. The red corpuscles, as they grow old, part with their colouring matter to the serum; from this it is taken up by the liver-cells, which transform it into bile-pigment; as such it is ultimately excreted in the fæces. Before it is thus removed, when retained in the gall bladder for any length of time, it undergoes further changes, passing through shades of yellow, green, brown, and black, which Shädeler terms respectively bilifuscin ($C_{32}H_{20}N_2O_8$), biliverdin ($C_{32}H_{20}N_2O_{10}$), biliprasin ($C_{32}H_{22}N_2O_{12}$) and bilihumin; bilifuscin differing from bilirubin in containing two atoms more HO, biliverdin from bilifuscin in containing two atoms more O,

biliprasin from biliverdin, again, by an access of 2HO, while bilihumin is a black, insoluble, very highly oxidised substance."

"The scale of colours enumerated above serves, as already stated, as a standard for the course of all other chromatases, whether physiological or pathological."

A careful study of these pigments will show the reason for this limited range of colour. If we examine the characteristics of the pigment layer on eggs, it is impossible to resist the conclusion that its presence has reference to the sun's rays. All organic objects which are liable to be exposed to the sun's rays are protected by pigment of one colour or another. This is the chief use of pigment in the animal world. In many animals the colours are adapted or modified for concealment, but their primary use is for protection from the glare of the sun. The delicate and tender ovum in particular requires protection. Professor Yung has shown the generating power of the sun's rays on the ova of frogs. In 1881, I read a paper showing that the pigment of frog's spawn was placed in the ovum itself to absorb the sun's rays as well as to protect the organism.¹ But the ovum of the more highly organised warm-blooded animals does not derive the stimulus required for its development from the rays of the sun but from the body of the parent. I think that this affords us sufficient reason for assuming that the use of the pigmented covering of the shell is to protect the sensitive ovum from being acted on by the sun's rays. If we make two perforations in a piece of cardboard, cover one with a piece of pigmented egg shell (*e.g.*, a rook's or blackbird's), and the other with a white one (*e.g.*, a pigeon's or a woodpecker's), and hold the cardboard up to the light, we see the great amount of protection afforded by the pigmented shell. True, the same end might be gained by thickening the shell, but it would have to be increased several fold to afford an equal amount of protection, and nature is never wasteful in material. Moreover, owing to the peculiar way in which the yolk is suspended by the chalazæ, the germinal spot is always uppermost, and consequently exposed to the sun's rays striking from above.

Mr Salvin noticed in Guatemala that humming-birds were much more unwilling to leave their nests during very hot

¹ *North Staffordshire Natural History Reports.*

weather, when the sun was shining brightly, than during cool, cloudy, or rainy weather.¹

I shall afterwards show that there is a direct relation between the amount of light to which the egg is exposed and the intensity of its pigmentation; that direct exposure to the sun's rays is necessary for pigment to acquire its full development; and that eggs deposited in sites protected from the sun's rays gradually lose their pigment layer.

If we examine these three shades from a purely chromatic standpoint, apart from any physiological views of their development, we shall see how admirably adapted they are for the purposes of protection and concealment.

1. Green is the colour we would naturally expect to find used as a protection for eggs. We know by experience that it has a peculiar softening influence on light. When it is present, it is always as a ground tint, uniformly spread over the surface of the egg. Most eggs are more or less covered with spots, blotches, or streaks, but these markings are never formed of green pigment. Many markings appear green to the eye, but this appearance is produced by the green ground tint being seen through a thin layer of black or brown. The spots in that case are of a darker green than the ground, but never deeper or richer. The most common tint is a bluish-green.

2. Red. If we see a reason for the use of green pigment as a protective layer on eggs, we can find an equally good one why red should be employed as the second or supplementary colour. In the chromatic circle all colours are arranged in pairs, and the colours in every pair are complementary to each other. When two colours are seen in juxtaposition, they mutually affect each other, both in colour and tone. A yellow object, for example, placed close to a blue one, will appear as if inclined to orange, while the blue object will seem to incline towards violet. But two complementary colours, such as red and green, do not modify one another's contiguity. They merely enhance each other's characteristics. Further, Professor Church remarks that green and red have a relation to each other which is different from that of any other pair of colours. "That there is something very peculiar in the relation of green to red," he adds, "may also be

¹ *Ibis*, 1864, p. 375.

concluded from the frequency with which these two colours are confounded by persons who suffer from colour blindness." The exact tint, which seems to be the basis of all the reds and browns found on eggs is a russet or orange-brown, and, if we examine the chromatic circle of Maxwell, this tint will be seen to be the complementary colour of the bluish-green, which I have just remarked is the usual ground tint. Red pigment is usually arranged in the form of spots, streaks, or blotches. Occasionally it is used as a ground tint—as in the grouse tribe—but then it is usually more or less speckled. It rarely if ever exhibits the smoothness or evenness of the green.

3. Black seems to be employed mostly as a tone giving neutral to enhance these two colours. Orange or red seen in juxtaposition with black is rendered rather lighter in tone and more luminous; green with black becomes more brilliant, but the black suffers in purity, and appears slightly tinged with a ruddy hue. The grey marking seen on many eggs, *e.g.*, the sparrow tribe, are produced by a light layer of black pigment.

Next to their limited range the variation of the colours of eggs in the same species is the most striking characteristic. In the eggs of several species, as gulls, terns, and guillemots, the range of lives extends almost from one end of the scale to the other. What a contrast with the colours of the birds themselves, where the colour of a few feathers in some instances constitute the difference between the species, or with lepidoptera where the pigmentation of a few scales determines the name of the insect. And not only do the eggs of birds of the same species differ, but those of the same individual vary almost to the same extent. Thus in a tern's nest, containing four eggs, I found one of a pale green colour and another of a deep reddish-brown. The other two were of intermediate tints. In this case the green egg had been the first laid and the brown one last.

Basing our theories on the development of pigments referred to above, which is generally accepted by physiologists, we would infer that green was the first colour which was developed in the eggs of the early species of birds. The eggs of the species extant support this conclusion. Green is the most common and most widely distributed colour. Schmidt states: "The more stubbornly a character is transmitted, or, what amounts to the

same, the greater the number of families, genera, and species over which a character is extended, the earlier did it appear in the ancestral stock." It is also, as has been shown previously, the colour best adapted for protection from the stimulating influence of the sun's rays, and there can be no doubt but that this is the primary use of pigment. Almost every egg which is laid in a situation where there is no need for concealment, but which is exposed to the sun's rays—*e.g.*, rooks, herons—is of a green colour.

Red or russet, and all the intermediate tints, appear to be developed chiefly for concealment, the different shades of brown showing in many instances perfect adaptation of the colour of the egg with that of its surroundings. This colour is chiefly exhibited on eggs which are deposited on or near the ground, as the waders', gallinaceous birds', larks', &c. Hewitson states: "We should scarcely expect to find the eggs of the crane so entirely different from those of all the other species which are most nearly allied to it in habit and in form. Whilst the eggs of all these species, with the exception of those of the spoon-bill, are either pure white or slightly tinted with colour, but always spotless, those of the crane are, on the contrary, richly coloured." This difference may be completely accounted for by the above theory, as the crane habitually breeds on the ground, whilst the others choose elevated sites. Compare also the eggs of the three species of divers, laid on the margin of the freshwater lochs in the north, with those of their congeners the guillemots, deposited on cliffs.

The coloration of the eggs of the Falconidæ are in some respects exceptional, depending on the nature of the food and other causes, which lie beyond the scope of the present paper.

When I examined eggs with reference to the amount of light to which they were exposed, I found that the ratio between the intensity of the pigmentation and the degree of exposure was very marked, and, indeed, almost startling. For example, the eggs of birds which breed early—as the thrush tribe, hedge-sparrow, &c.—have well-developed ground tints; whilst those of the later breeders—as the green finch, linnet, &c.—laid after the leaves are out, and therefore screened from direct sunlight are more faintly coloured. My own experience is that exposure or

shelter from the sun's rays plays an important part in the selection of a site for nidification, by the parent bird.

It may be laid down as an almost universal law in ornithology, that eggs which are deposited in situations exposed to the sun's rays are much darker in colour than those laid in nests protected from direct sunlight. They almost invariably possess a well-developed ground tint. Some, *e.g.*, the heron and the hedge-sparrow, are spotless, but most show markings of some kind.

Eggs laid in shaded nests, *e.g.*, the yellow-hammer and the green finch, possess a faint ground tint, and the markings are usually smaller and lighter than in the preceding.

Eggs laid in covered nests, as the tits' and wrens', usually present faint spots in a white ground.

Eggs which are wholly excluded from light, as woodpeckers' and kingfishers', are almost invariably pure white.

Not only does direct sunlight seem necessary for the pigment layer to acquire its full development, but there is also strong evidence that all white and faintly coloured eggs have undergone or are undergoing a process of decolorisation when the protection afforded by the pigment layer is no longer required. This is in accordance with the laws of physiology. If any tissue or organ loses its function it will gradually waste, and finally disappear. Moreover, it has been shown by evolutionists that the lost organ is apt to appear as a variation, or as a rudimentary and useless appendage: many eggs, therefore, show rudimentary pigmentation, and colour appears sometimes as a variation in eggs which are normally white. Eggs have been divided by Wallace into white and coloured, spotted and unspotted; there is, however, an unbroken series between white eggs and those which are highly pigmented and spotted. Further, the eggs of several species would have to be included at one time under the former category, and at another under the latter. For instance, the egg of the white-tailed eagle is usually white, but occasionally it presents well-defined markings. The egg of the puffin is as often colourless as it is pigmented. That of the whinchat is of a bright blue-green, sometimes spotless, sometimes faintly speckled at the large end with rust colour.

It has been stated that white and light coloured eggs are found

in dark and sheltered situations because colour is not necessary to conceal them from observation. The fact has, however, been overlooked, that eggs laid in elevated sites, as gulls', rooks', herons', &c., have well-developed colours, although they can be of no use for concealment. Want of the stimulus of the sun's rays alone causes the colour to fade or disappear.

When one (or one or two) species in a family, where the majority lay deeply pigmented eggs, lays either a white egg or one faintly coloured, we invariably find that it differs from the others in its mode of nidification, depositing its eggs in some place protected from the light, whilst its relations lay in exposed situations. In this case there is what may be termed a specific decolorisation, the loss of pigment affecting the individual species alone, and not extending to the other members of the family.

When the whole of a genus or family lay white eggs, we find that either all, or the majority of the species, deposit their eggs in places protected from the light. In this case there appears to have been a generic decolorisation affecting the group as a whole, the pigment having become obsolete at a much earlier period than in the preceding case, probably before the differentiation of the family into the existing number of species.

SPECIFIC DECOLORISATION.

In examining the evidence of decolorisation of eggs, it will be necessary to enter somewhat into the details of the modification of several groups of birds to show the various ways in which the eggs are protected from the stimulating influence of sunlight. With reference to this, eggs may be divided into three classes viz. :—(1) those laid in holes or covered nests, (2) those which are covered by the parent bird with leaves, weeds, &c., and (3) those covered by an incrustation of calcareous matter. The eggs of nocturnal birds are white or faintly coloured but are included in the above.

1. Eggs deposited in holes or covered nests.

The egg of a woodpecker, or any bird where the whole of the family lay white eggs and are identical in their mode of nesting, affords no evidence of decolorisation. But when we find one species only in a family laying in a covered nest, and

its eggs white or faintly coloured, whilst those of the other members are laid in open sites and are highly pigmented, we may fairly argue that the pigment covering has degenerated or vanished. Thus all the thrush family lay richly coloured eggs in open sites, whilst the dipper, a closely allied species, lays a white egg in a domed edifice. The egg of the black redstart, one of a genus where all the other members lay coloured eggs, is exceptionally pure and white. Again, the auk tribe is notable for laying bright coloured eggs on bare ledges on the cliffs; whilst the puffin, one of the family which breeds in rabbit holes, lays an egg, described by Hewitson as "sometimes spotless, but more frequently marked with various tints of colour, but so very faint and indeterminate as to appear as though they were seen through the shell." The wheatear is a good example of an egg which has undergone almost complete decolorisation. One of the most interesting cases is that of the Virginian quail. This is the only one of our gallinaceous birds which builds a dome-shaped nest, or, indeed, may be said to build any nest at all. Yarrell states that the eggs are white, although Hewitson figures one of a faint buffy tint, with minute spots. All the rest of this order lays eggs with a well-developed ground tint, and usually richly covered with dark-coloured markings.

2. Eggs covered by the parent bird with leaves or other vegetable matter.

There is no doubt but that a loss of pigment has resulted from this mode of concealment. It is interesting to speculate on the reasons which have led certain birds which breed on the ground to adopt this method of protection, whilst others trust to the colour of the eggs. In the grebe tribe it seems the only method possible. Protective coloration of the eggs would be a much less effective mode when they are deposited on the top of a large and prominent heap of decaying water plants; and it would be impossible for them, on account of their peculiar wings and legs, to escape from the nest unless it were close to the water's edge. "It would seem that whatever they do must be done in the water," writes Naumann; "they cannot even rise upon the wing without a preliminary rush over the surface of the lake; from dry land they cannot commence their flight." The loss of pigment is complete in the grebes, as it is probable

that the wet decaying vegetation shuts out the light more completely than the loose dry materials employed by the ducks, pheasants, &c.

In the duck tribe this method has probably been adopted because of the size and large number of eggs laid. Protective coloration could not have afforded sufficient concealment for eight or ten or even more large eggs. The amount of decolorisation varies in this tribe. In some instances, as the eider duck, the egg is of a pale asparagus green, in others it has only a very faint greenish hue, whilst in the shieldrake, which breeds in holes, the loss of pigment is complete; the egg being of a "smooth shining white."

In both the above groups the whole of the family adopt the same mode of concealment, but why should the eggs of the pheasants and partridge be correct, whilst those of the grouse are laid openly? The two former birds breed in sheltered woods and hedgerows, the latter on bleak and exposed moors. If the grouse covered its eggs with dead vegetable material it would soon be carried away by the strong winds which sweep over the moors.

3. *Eggs covered by an incrustation of calcareous matter.*

Only three British birds' eggs are coated with this peculiar chalky substance, viz., the cormorant, the shag, and the gannet. The hard shell beneath is of a faint bluish-green colour in the two first-mentioned species; in the last it is usually pure white, but sometimes tinged with blue-green.

GENERIC DECOLORISATION.

The fact that certain birds deposit white eggs in fully exposed situations has been pointed out as proofs that the coloration could have no reference to the exposure to light. But no notice has been taken, as far as I am aware, of the fact that all these instances occur in families where the majority of the species breed in holes or dark places. In this case decolorisation must have taken place at a much earlier period in the life-history of the family or genus than in the preceding instances. They are probably descended from some ancestor which bred in holes; and the change to open nests in a few members of the family taking place long after the colouring matter had disappeared

has not been followed by a restoration of the pigmentary covering. For proofs that pigment had at one time existed in these groups, we must look to the eggs of allied species. They occur in the owls, the pigeons, and the petrels.

"There is a strong and perfect similarity amongst the eggs of the different species of owls," writes Hewitson, "which we could scarcely expect to find in the eggs of birds which differ so much from each other in their mode of breeding. The eggs of those species which are deposited in the hollows of old trees and deserted ruins, and those which are found on the bare sod, and exposed to the broad light of day and the pelting storm, are alike without colour." But the large majority of the species breed in dark places, and, being nocturnal in their habits, all have a tendency to avoid light. Now their nearest congeners, the harriers, which link their family with the Falconidæ, bear a close resemblance to them in many points, *e.g.*, the loose and flocculent character of the feathers, and the circular arrangement of those about the face; and the affinity on comparing the skeletons of each is most decided. In the coloration of the eggs also the resemblance exists, the eggs of the harriers being white, or sometimes a pale skim-milk colour, more rarely spotted and smeared with brown.

All the Columbidae, or pigeon tribe, lay two pure white oval eggs. All, however, lay in crevices in rocks, hollow trees, deserted rabbit burrows, or dense thick trees or bushes. This, together with the fact that the nests of the arboreal members are crude platform-like structures, quite unlike those of any other bird, show that they are descended from an ancestor which bred in holes. One of the Australian ground pigeons is said to lay buff-coloured eggs. The nearest ally to this order, Pallas' sand grouse, lays three oval eggs, similar to a pigeon's, but coloured like a plover's.

The petrels are all more or less nocturnal in their habits, and all lay white eggs.¹ The fulmar deposits its egg openly, on ledges on the cliffs, but the other members of the group lay in crevices in the rocks, under stones, or form burrows to the depth

¹ Since this was written Mr Bladen has called my attention to a mass or ring of very faint markings near the large end of the eggs of some of the petrels. These, which appear to have been hitherto overlooked by writers on the subject, are the best examples I have yet seen of rudimentary pigmentation.

of two or three feet. All the rest of the Laridæ lay richly coloured eggs.

It will be seen from the above that the decolorisation takes place in three ways. In some—swallows, wrens, tits, &c.—the ground tint disappears first, leaving the egg more or less thickly marked with small light coloured spots; in others—starlings, little auks, &c.—the markings vanish first; while in a third class—puffin, hen-harrier, &c.—both ground tint and spots appear in a rudimentary degree.

In this paper reference has only been made to the eggs of British birds, not only because the fauna of these isles form a very complete and typical group, but because the views adduced are based solely on the study of thousands of specimens of British eggs in my own and other collections, and upon observations made on the moors, in the woods, and by the seaside.

Evidence has been brought forward to show that the pigmentary coat on birds' eggs came into existence at a very early period in their life-history, and existed in the eggs of the progenitors of all the extant species. It has also been shown that the range of colours on birds' eggs is very limited, but follows the usual course of pigmentary changes; that the pigment is unstable and variable, making the process of change and decolorisation a simple one; and that its primary use is for protection from the solar rays, but that it afterwards became modified for concealment.

Lastly, it has been shown that eggs acquire a highly developed pigmentary layer, or lose their pigment entirely, according to whether they are exposed to the full glare of the sun or laid in situations inaccessible to its rays, and that the intermediate degrees of coloration are in direct ratio to the amount of light to which the eggs are exposed.

The two causes which determine the coloration of eggs—protection from the sun's rays and concealment from observation—act conjointly; they are not antagonistic like natural selection and sexual selection. The limited range of colours shows that natural selection alone operates. Darwin states that, in regard to structures acquired through ordinary or natural selection, there is a limit to the amount of advantageous modification in relation to special ends; but in regard to structures acquired

through sexual selection there is no definite limit; so that, as long as the proper variations arise, the work of sexual selection will go on. That the causes are different from those which produce the colours of the birds themselves, is shown by the fact that eggs from tropical regions do not surpass in brilliancy of tint those of more temperate climes.

THE CONNECTION OF THE OS ODONTOIDEUM
WITH THE BODY OF THE AXIS VERTEBRA. By
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Chirurgery in the University of Dublin.*

(This paper was read before the Biological Section of the British Association
in Aberdeen, September 1885.)

THE point in connection with the os odontoideum which I have to bring under the notice of this section is a small one, but still it is not without some interest and also morphological significance.

For some time past I have been engaged in an investigation into the curves of the spinal column of man and the apes, and in carrying out this work I have made mesial sections of a large number of frozen human spines. Very soon my attention was attracted to a small lenticular-shaped plate of cartilage, which seemed in almost every case to be interposed between the os odontoideum and the body of the axis vertebra. On all sides it was surrounded by bone, so that it could only be brought into view by means of section. To obtain a proper conception of the significance of this cartilaginous plate, it will be necessary that we review some points in connection with the development of the axis vertebra, and its tooth-like process.

The identity of the os odontoideum with the absent body of the atlas is, so fully and satisfactorily established, that it is unnecessary for me to do more than merely allude to it. Whilst this is the case, however, in man, the os odontoideum and the body of the axis in their early condition form one continuous cartilaginous mass, with no external marking by means of which the one can be distinguished from the other. Both are traversed by the notochord and the only evidence of their separate nature is to be found in a notochordal swelling or dilatation at their point of junction.¹

The manner in which this cartilaginous mass is ossified is

¹ Robin, *Evolution de la Notocorde*, Paris, 1868. Müller, *Ueber das vorkommen von Resten der chorda dorsalis beim Menschen nach der Geburt*, &c., &c. *Zeitschrift für rat. med.*, N.F., Band 11.

very instructive. The body of the axis is converted into bone by one primary centre and an epiphysary lamina, which is formed upon its lower surface. The os odontoideum ossifies by two lateral primary centres, which soon fuse, and an apical epiphysary centre for the summit. The last undoubtedly represents the upper epiphysary plate of the atlas vertebra.

The apparent differences, then, between the ossification of the os odontoideum and the centrum of the axis on the one hand, and that of the corresponding parts of the vertebræ lower down on the other, resolve themselves into two.

1. The absence of an epiphysary centre for the lower surface of the os odontoideum, and for the upper surface of the body of the axis vertebra.

2. The double primary centre which appears for the ossification of the odontoid.

Both of these discrepancies can be more or less easily explained. With regard to the first, Macalister¹ has described both of the absent epiphysary plates as being present in the axis vertebra of the *Balaenoptera rostrata*, and he likewise states that in some cases they can also be detected in man. Further, Humphry has observed and figured one of the absent nuclei in the rabbit.²

The second point of difference is more difficult to understand. It is true that many anatomists deny the double character of the odontoid centre; they see no material difference between this centre and that of the other vertebral bodies. Thus Gegenbaur, Henle, and Blandin give expression to this view, and Robin³ insists strongly upon it. It is a conclusion, however, which we cannot adopt. On the other side we range Meckel, Luschka, Sappey, Cruveilhier, Quain, Macalister,⁴ and several

¹ Macalister, *Jour. Anat. and Physiology*, vol. iii. p. 54.

² Humphry, *The Human Skeleton*.

³ Gegenbaur, *Lehrbuch der Anatomie des Menschen*, 1883. Henle, *Handbuch der Anatomie des Menschen; Erste Abtheilung, Knochenlehre*, 1871. Blandin, *Nouveaux Éléments d'Anatomie*, 1838, vol. i. p. 39. Robin, "Sur le développement de vertèbres," *Jour. d'Anat. et Phys.*, Paris, 1864.

⁴ Meckel, *Descriptive and Pathological Anatomy* (translated by A. S. Doane), 1839. Luschka, *Die Anatomie des Menschen. Erster Band*, p. 32, 1863. Sappey, *Traité d'Anatomie*, Tome premier, p. 312, 1876. Cruveilhier, *Anatomie descriptive*, 1871, vol. i. p. 73. Quain's *Anatomy*, 9th edition. Macalister, *loc. cit.*

others, all of whom believe in the originally double condition of the odontoid ossific centre. In support of this I may bring under the notice of the section an extremely interesting specimen of an axis vertebra, from the Pathological Museum in Trinity College, Dublin, in which the os odontoideum is double.¹ In other words there are two distinct odontoid processes springing from the upper surface of the body of the axis vertebra. Such a condition could only have been produced by the presence of two ossific centres which have failed to unite.

Granting, then, the double centre for the odontoid, how can this deviation from what is generally considered to be the typical mode of ossification of a vertebral body be accounted for. Humphry has offered the best solution of the question. It is not uncommon to find one or more vertebral centra cleft into two lateral parts, clearly showing that they have been ossified from two centres. The very specimen to which I have alluded is an example in point, because not only is the odontoid bone cleft into two, but so also is the body of the axis. In view of abnormalities of this kind, Humphry has been led to suppose it possible for the ossification of a vertebral body to take place by two twin centres which fuse almost immediately after their appearance.

For a considerable time the os odontoideum is separated from the body and pedicles of the axis vertebra by a layer of cartilage. It is essential that we should study the changes which this plate of cartilage undergoes. The accounts given of these by different authors are at utter variance with each other

According to Henle,² Cruveilhier,² and Quain,² we are led to believe that the cartilage disappears at the third year, and that the osseous union of the odontoid and axis vertebra is then complete; according to Sappey² and Robin² the union is accomplished more slowly, and is not perfected until the sixth or seventh year; Humphry, on the other hand, delays the consolidation until puberty.

The observations which I have made on this point would seem to indicate that it is not until old age is attained that

¹ This specimen has been figured and described in its pathological aspects by Prof. Bennett in the *Trans. Path. Soc. Dublin*, vol. vii. p. 117.

² *Loc. cit.*

complete osseous union between the os odontoideum and the body of the axis takes place.

In sixteen out of eighteen axis vertebræ which were obtained in the Trinity College practical anatomy room, without reference to age or sex, a small disk of cartilage was found on section, marking the line of separation between the odontoid and the second vertebra. In dealing with dissecting room subjects, it is extremely difficult in Dublin to obtain reliable information regarding the age of any particular individual. Three of the specimens examined I have been obliged to eliminate, as I was quite unable to arrive at any knowledge of the age of the subjects from which they were taken. Of the remaining fifteen (which include the two bones in which the cartilage is absent) I was only able to ascertain the precise age of two; whilst in the case of the others notes were made of the probable age of the subjects as they came in.

The fifteen vertebræ which remain may be divided into three groups according to their age.

GROUP I.—*Axis vertebræ obtained from subjects varying from twenty-four to fifty years of age.*—This group comprises six vertebræ—two from females and four from males. The youngest specimen was taken from a girl of about twenty-four years old; the others were obtained from subjects varying in age from forty to fifty. In all the members of this group the cartilaginous plate was present. In sagittal section its average length was 4 mm., and its average thickness 2 mm.

GROUP II.—*Axis vertebræ obtained from subjects varying in age from fifty to sixty years.*—In this group there are only three specimens—all from females. In each the plate of cartilage is present, and its average dimensions are the same as in Group I.

GROUP III.—*Age ranging from sixty to seventy years.*—Six specimens—two males and four females. In four members of this group the cartilaginous disc was present, and in sagittal section its average dimensions were: length, 3 mm.; thickness, $1\frac{1}{2}$ mm. In two it was absent; one of these is marked as being taken from a subject seventy years old, whilst in the case of the other the age was put down as sixty-five. They were the oldest specimens examined.

But how can these facts be reconciled with the statement
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made by some that the os odontoideum unites to the axis at the third year, and by others that the two bones are consolidated at the seventh year. Both of these assertions are, from one point of view, more or less correct. From the third to the fifth year the base of the odontoid joins on each side with the pedicles and the body of the axis, obliterating at these points the intervening cartilage. The middle portion of the cartilaginous plate, however, still remains and extends from the anterior to the posterior face of the bone. At the seventh year (often much later) consolidation takes place, first in front and afterwards behind, and the cartilage is thus entirely cut off from the surface. But the ossific union is restricted to the periphery; the further process is extremely slow, and is apparently not completed until an advanced age is attained. Robin, therefore, is in error, in so far as he has mistaken peripheral consolidation for complete union. Cruveilhier, Henle, and Quain, with much less reason, mistake lateral consolidation for complete union. Humphry's account of the ossification of this bone is more accurate. He defers complete consolidation until puberty, and he speaks of a space which remains in the centre, which resembles the intervertebral spaces seen in section of the sacrum. If a dry bone be cut with a fine saw, this space can, as a rule, be made out; it is the cavity which contained the cartilaginous plate.

In order to determine the nature of the disk of cartilage which persists so obstinately in the interior of the axis vertebra, I decalcified the specimen I obtained from the girl of twenty-four, and cut the odontoid process and the body of the axis in the longitudinal direction for microscopical examination. The cartilage was then seen to be of the hyaline type throughout its entire extent. In some of the sections faint traces of a feeble and sluggish ossific process might be detected around the margins of the cartilage. Not a vestige of the notochord could be discerned. Robin states that the notochordal swelling, at this point, disappears when ossification sets in, and that it is replaced by a small mass of fibro-cartilage which shades off on all sides into hyaline cartilage. Henle also refers to a fibro-cartilaginous layer in the very young bone. There is not the slightest appearance of this in the sections which I have

made of the adult bone. This is strange, seeing that fibrocartilage is generally looked upon as the descendant of hyaline cartilage, and it is difficult to conceive a reverse development.

The morphological significance attached to the obstinate persistence of this cartilaginous plate in the axis vertebra of man is very apparent:—

1. The foreign character of the odontoid bone as an element of the axis vertebra is more forcibly insisted upon.

2. It establishes a condition of the axis vertebra which is not so far removed from that of the Monotreme and Thylacine,¹ in which the union between the odontoid and axoid body is exceedingly late—if indeed it ever occurs at all.

3. It establishes a more obvious basis for comparison with those reptiles in which the odontoid persists as a separate bone.

¹ *Report on The Marsupials*, by D. J. Cunningham, in the Reports of H.M.S. "Challenger," Zoology, part xvi., 1881.

THE SKELETON IN GEOCOCCYX. By R. W. SHUFELDT,
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VII., VIII., IX.)

WHEN I came to North-Western New Mexico, early in the autumn of 1884, I expected to enter the very heart of the home of *Geococcyx californianus*. Much to my surprise, however, after a residence of seven and more months in the country, not a single individual of this species has rewarded my many mountain and prairie excursions. Not to be foiled in securing specimens of its skeleton to complete my papers upon the osteology of the birds of this country, and more especially those peculiar to it, I sent a considerable number of letters to collectors in Texas, Arizona, and California. Many weeks of patient waiting brought me answers to only three of these, and all from the last named state. One said the bird was no longer to be found in his neighbourhood, while from my other two correspondents I secured each a skeleton, but both informed me that owing to the great demand on the part of collectors for the "Road Runner," it was rapidly becoming a rare bird in localities where formerly it was very abundant. My last specimen, an old male, afforded me a perfect skeleton, and from it I made the drawings which illustrate this account, while the second bird, though not meeting my expectations so fully, still gave a skeleton, which has proved of great service to me, in the way of comparison and verifying points present in my type.

The aim of this memoir is simply to give a full description of the skeleton of *Geococcyx*, and in it I will undertake but few comparisons. Some day in the future it is my hope to enter more extensively upon the entire anatomy of this form, so full of interest to all biologists.

Of the Skull (Plate VII. figs. 1, 2, 3, and 4).—In *Geococcyx* we find the osseous superior mandible with a gently curved and rounded culmen, the curve increasing very modestly as it

approaches the apex. This part of the skull has a broad base, being both deep and wide in the rhinal region, while on all aspects it tapers gradually to the slightly decurved tip. Its buccal surface is flat, with cultrate edges somewhat raised above the general plane behind. Posteriorly, this face is encroached upon by the palatines and maxillo-palatines. Turning to the lateral surfaces of this mandible (fig. 1) we find them for the most part to be slightly convex throughout their extent; the only exception to this being seen in the depressions which are found, one over each of the scale-like projections that close the hinder two-thirds of either nostril. These last mentioned openings are of a sub-elliptical outline, placed longitudinally nearer to the edge of the beak than its culmen, and just posterior to its middle. They do not directly, communicate with each other, but are external apertures, in this bird, of osseous tubes, one on either side, which are produced backwards nearly to the rhinal chamber, being encased in the loose osseous spongy mass that almost fills the otherwise hollow superior mandible of *Geococcyx*.

The cranio-facial hinge enjoys considerable mobility, and its position is clearly indicated by a transverse track. Mesially, this region is depressed, and may show the last sutural traces of the nasal processes of the premaxillary therein. Each nasal bone has been so completely met by the various surrounding elements, that, save its hinder margin, its boundaries are hard to define in the adult bird (figs. 1, 3). To the inner side of each, and just beyond the cranio-facial track, we observe on either side a small circular foramen, which is constant, and is to be found in like locality in *Ceryle*.¹ All three sides of this osseous superior mandible is more or less marked by anastomosing venations, and a few perforating foramina are always seen near its apex.

A *lacrymal* in *Geococcyx* is an unusually large bone, though a light one, due to its very open cancellous structure within, and its being, perhaps, pneumatic besides. Superiorly, it articulates with the frontal and nasal, principally with the last on the lateral aspect, though it departs from it some time before reaching its

¹ "Osteology of *Ceryle Alcyon*," by the author, *Jour. of Anat. and Physiology*, April 1884, Plate XIV. figs. 1 and 2, *nf*.

lowest point, where a slit-like interval is seen between the two bones. Below, its broad rounded margin is placed obliquely, its outer and at the same time posterior end, resting upon the upper side of the maxillary, while its inner and anterior end being elevated just above the superior surface of the corresponding palatine.

The posterior aspect of the lacrymal is concave from above downwards, in conformity with the somewhat globular concavity of the orbit, while anteriorly it is correspondingly convex in the same direction. It lies in front of the broad, quadrilateral ethmoidal wing which overlaps it, the two forming a very complete partition between the orbit and rhinal chamber; the bone under consideration closing the outer third of the space.

The ethmoidal wing, the form of which I have just given, is pierced above, immediately beneath the frontal bone, by two elliptical foramina, the inner one being the larger, and both being placed vertically. They probably transmit the olfactory nerve and vessels to the rhinal space.

This "pars plana" has, like the lacrymal, also a somewhat cancellous internal structure, the plate being moderately thick. Its lower and outer margins are concave and smoothly rounded off.

The expanded anterior extremity of a *maxillary* is immovably sandwiched in between the nasal above, and the posterior dentary process of the premaxillary beneath. Its rod-like extension behind forms about the anterior third of the very straight quadrato-jugal bar. The horizontally expanded end alluded to is quite ample, and may be perforated by numerous foramina. Its maxillo-palatine development will be described when speaking of the under side of the skull.

The remainder of the quadrato-jugal bar becomes gradually larger and club-shaped as it nears the quadrate bone, to rather abruptly turn inwards as it reaches it, and is inserted in a vertical notch in the usual apophysis of that element, which projects directly outwards to meet it (fig. 3).

With respect to the *quadrate*, we find that its orbital process is very broad and flat, being at the same time very short. The body of the bone is also broad, while its mastoidal apophysis is twisted in a way common to many other birds, and supports at its summit two articular heads with a distinct valley between

them. At the inferior aspect of the mandibular foot, there are two condyles for articulation with the lower jaw. The inner and smaller of these is hemi-ellipsoidal in form, with its major axis in the same straight line that constitutes the longitudinal axis of the corresponding pterygoid. If this axis be produced the other way, it is found to be at right angles to the long axis of the other and larger facet of the mandibular foot of the quadrate. Rather a broad notch separates these two condyles from each other.

The quadrate is a thoroughly pneumatic bone, and a large foramen is always found upon its posterior aspect half-way between the mastoidal head and the mandibular foot.

Both the sphenotic and mastoid processes are well developed in this bird; they are of about an equal size, the first being directed downwards, and the last downwards and forwards. Between them, and carried well to the rear, is a sharply defined and rather deep crotaphyte fossa. It is separated from a like depression of the opposite side, by an interval of one and a half centimetres. These crotaphyte fossæ are fully as well marked in *Geococcyx* as they are in many of the *Laridæ*, and better than they are in some members of that group of birds, better for instance than they are in *Chroicocephalus philadelphia*.

Owing to the great breadth of the frontals, the orbit is completely sheltered above by an arching roof; the outer periphery of which is concave inwards, and bounded by a sharp edge. This orbital vault usually shows posteriorly a few perforating foramina.

The *rostrum of the sphenoid* is pneumatic and rounded for its entire length beneath. It barely extends beyond the broad ethmoidal wings in front, and ascends but little as it proceeds in that direction.

The *inter-orbital septum* is a thin partition of bone, which always possesses a considerable quadrilateral vacuity near its centre. This usually merges with the foramen for the exit of the optic nerves (fig. 1), while the small foramen for the exit of the *oculi-motor* remains distinct.

As might be expected from what has already been said about the orbit, we find its hinder wall also very broad, and generally concave forwards. At its usual site a distinct, irregular foramen

of some size is found for the exit of the *olfactory nerve*, and this branch passes forwards in the living bird in a shallow channel on the inter-orbital septum beneath the frontal, for its entire length, where these two elements are united. It leads to the inner and larger of the two foramina that were described above, as occurring over the *pars plana*.

Before leaving this side view of the skull, it will be as well to notice the large, luniform sesamoid that occurs in the ligament that passes from the quadrato-jugal to the hinder border of the articular cup of the mandible. This sesamoid is present on both sides, and in all the skulls of *Geococcyx* that I have ever had the opportunity of examining.

On the superior view of the skull we are to note the form of bony lamina that partially close in the external narial openings from behind; the position of the two small circular foramina beyond the cranio-facial hinge; and this fronto-lacrymal region generally. From this aspect, we also see the small foramina that pierce on either side the orbital roofs behind. Mesially, and between these latter, a shallow, longitudinal groove marks the cranial vault. Posterior to this again we find a smooth, globular, and ample parietal region. The crotaphyte fossæ may likewise be discerned from this upper aspect, and a glimpse obtained of the supra-occipital prominence. It is also useful in showing the manner in which the quadrato-jugals articulate with the quadrates.

Viewing the skull of *Geococcyx* from beneath, we find, anteriorly, the broad, flat surface, already spoken of, which forms the lower face of the superior mandible (fig. 4).

Following this back we come to an elongated median vacuity, that separates the anterior terminations of the maxillo-palatines. This aperture has irregular, jagged edges, and through it we may see some of the open, spongy bone tissue that partially fills the hinder portion of the core of the superior mandible. At the sides, the posterior processes of the dentary parts of the pre-maxillary overlap the maxillaries. They are long and triangular, with their apices to the rear.

Returning to the *maxillo-palatines* we find them to be, upon this aspect of the skull, two very sizeable, elongated, subcylindrical masses, composed of an internal spongy tissue, but encased in an outer covering of an extremely thin layer of compact

tissues. They lie parallel to each other, and to the median plane, nearly filling the interpalatine space. Anteriorly, they are separated by the vacuity already described, while behind their free and rounded extremities slightly diverge from each other, they being in contact in the median line for the middle thirds of their lengths (fig. 4). From their upper sides is developed a mass of open, spongy tissue; this is continuous with a similar structure that is found within the superior mandible; it reaches out on either side, to abut against the inner surfaces of the nasals; it joins the horizontal plates of the maxillaries, and finally supports a median vertical plate of bone that stands just beyond the rhinal chamber proper, this latter space being free from its encroachment, as it is from any development of the *ethmoid* behind, beyond its lateral wings.

The anterior half of either *palatine* is quite a broad, flat, horizontal plate, the distal end of which indistinguishably fuses, and is directly continuous with the horizontal portion of the premaxillary. To its inner side also, in this locality, it completely anchyloses with the corresponding maxillo-palatine (fig. 4). For the most part, however, its inner and outer edges are free, not coming in contact by the inner one with the maxillo-palatine, though it is parallel to it, and separated by an extremely narrow interval, while its outer one neither touches the lacrymal nor the maxillary, but occupies a plane inferior to both.

The posterior half of a palatine also lies mainly in the horizontal plane, but its under surface is a concave one, and its upper correspondingly convex. Its outer free edge, directly continuous with the outer edge of the anterior half of the bone, sweeps by a gentle curve round the "postero-external angle" of the palatine to its head.¹

¹ Professor Huxley, in his "Classification of Birds" (*Proc. Zool. Soc.*, April 11, 1867, p. 444) says:—"In *Geococcyx* the principle of construction is quite the same [as it is in *Cuculus canorus*], but the postero-external angles of the palatines are distinctly indicated." In the two excellent skulls of adult specimens of this bird before me, as well as those I examined in the collection of the Army Medical Museum at Washington, the postero-external angles are rounded off in the manner above described, and the presence of a process is in no way indicated whatever, and I must believe Professor Huxley had in hand, the time he penned the words I have quoted, an imperfect and perhaps broken skull of *Geococcyx*. (See also my remarks upon this point in my "Osteology of *Ceryle alcyon*," *Jour. of Anat. and Phys.*, April 1884, p. 289).

The inner free edge of the bone extends from the head to the apex of a small pointed process in front. For nearly its entire length it is parallel to the corresponding edge of the palatine of the opposite side, from which it is separated by an interval of something like a millimetre or rather more. From this edge the surface curves outwards and back, forming the "ascending process" of the palatine. This terminates in another longitudinal straight margin, which is applied to the corresponding one of the opposite palatine, and both unite to form the usual groove at their upper aspects for the rostrum of the sphenoid. These latter opposed edges also extend from the palatine heads, likewise in contact mesially, to a common anterior process. This latter is nearly opposite the anterior end of the rostrum, and from its extremity in front projects a free, needle-like, and rudimentary *vomer*, of some four millimetres in length. It does not come in contact with the maxillo-palatines, but lies above the interval formed by their slightly diverging posterior extremities, and is freely articulated with the palatines at the point from which it springs, and in the manner described. This diminutive vomer is equally well developed in both my specimens of *Geococcyx*.

A *pterygoid* is a nearly straight and slender bone, and shows not the slightest evidence of the development on its shaft of an apophysis, and indeed there is no necessity for such, as the basi-ptyergoidal processes are entirely absent in this bird; and the pterygoids when *in situ* occupy a lower plane than the basi-temporal region, as well as being at some distance in front of it.

These bones articulate with each other anteriorly and with the opposed palatines; from this point they diverge at an angle of about 85° , each to meet the usual facet upon the corresponding quadrate at the base of the inner and smaller condyle on that bone.

The *basi-temporal region* is elevated above the prominent and raised boundaries of the auricular apertures; it is narrow and smooth and lies for the most part in the horizontal plane. In front it presents for our examination a thin tip of bone, arching over the common aperture of the Eustachian tubes.

Beyond this it contracts to form the sphenoidal rostrum, a considerable portion of which is unoccupied before we reach the pterygoidal heads. This allows these bones not a little

backward play in the recent specimen, an action which is quite possible from the more than ordinary mobility enjoyed on the part of the cranio-facial hinge.

Either external auricular conch is a capacious fossa, well-defined by a raised and bounding thin wall of bone, with its free edge curled in all around. At the base of either of these fossæ, we see strong osseous trabeculæ converging to a point near the centre, to support the double concave facet for the mastoidal head of the quadrate. These stand between the Eustachian entrance and the passage to the middle ear.

If the plane of the basis cranii be produced posteriorly, and the plane of the occiput and foramen magnum extended to meet it, we find the latter makes an angle with the first mentioned plane of about 48° , while the long axis of the fairly well-developed supraoccipital prominence would be perpendicular to it. In form the *foramen magnum* is broadly cordate with its apex above; the *occipital condyle* at its lower margin is small, sessile, and hemispherical in outline, being so placed as to encroach upon the foraminal periphery for about one-third of the condylar arc.

Points of interest within the brain-case are seen in the presence of a strongly marked longitudinal sinus, and the unusual thickness of the walls of the sella turcica; its fossa, though deep, being quite small, while at its base we find a double entrance for the carotida.

As a whole, the skull of *Geococcyx* is a delicate and a very light structure for its size, air gaining thorough access to most of its parts.

The *mandible* (figs. 1 and 2), seen from superior aspect, has the typical V-shaped form, with an extensive symphysis, which is scooped out longitudinally above. Either ramus is not deep in the vertical direction, while its upper and lower margins are prominent and rounded, the former, however, becoming sharp as it approaches the symphysis, which condition is sustained to the mandibular apex.

The ramal vacuity is large and occupies its most usual site; in outline it is an elongated ellipse, but its anterior third is encroached upon by a thin plate developed on the part of the dentary element. An articular end is considerably concave

above; and presents two facets for the condyles of the quadrate; its inturned process is much tipped up, while the usual pneumatic foramen is seen near its apex. Below, its convexity conforms with the concavity of the articular excavation at its upper side, and its angle behind is obliquely truncate from above downwards in the forward direction.

Beyond an articular end, on the superior ramal border, we find, on either side, the coronoid process but feebly developed, and single.

When the osseous mandible is articulated *in situ* with the remainder of the skull, its tip does not extend quite so far forwards as does the apex of the superior osseous beak, a condition present in the skulls of most *Coracomorphæ* and other groups.

In the *hyoidean apparatus* (fig. 8) we find fully the anterior two-thirds of the glosso-hyal represented by a thin stripe of cartilage; while behind, where it ossifies in front, the usual median foramen is seen, having an elliptical outline. Posterior to this, on either side, the strongly marked cerato-hyals project outwards and backwards.

First and second basi-branchials do not anchylose with each other, the former being short and thick, the latter about half as long again, and tipped off behind with cartilage.

The elements of the thyro-hyals are long and slender, they likewise terminate in cartilaginous tips, and curve up behind the skull in the manner most usual among birds.

Of the remainder of the Axial Skeleton—The Vertebral Column.—This column presents us with eighteen movable vertebræ before we arrive at the consolidated pelvic sacrum. This latter contains eleven more segments, thoroughly united together and firmly joined to the iliac bones. Finally, we find five vertebræ and a large pygostyle in the skeleton of the tail of *Geococcyx*.

In the cervical region we pass twelve vertebræ before we come to the first one of the series that bears a pair of free ribs; the thirteenth and fourteenth both possessing these appendages, and in both they are well developed, though not reaching the sternum, through the intervention of costal ribs. The pair on the fourteenth vertebræ has the epipleural processes fully as large as they are in the dorsal series; they are absent entirely, however, on the first pair of free ribs.

Returning to the *atlas* we find this segment rather delicately constructed, though assuming the form the bone usually offers among Passerine birds. Its neural arch is narrow antero-posteriorly, though the canal is capacious. A perforation is seen at the base of the articular cup for the occipital condyle, which cuts through the superior margin of this little concavity. The centrum is small and does not develop anything that might be called an hypapophysis. On the *axis* vertebra we note the presence of a low, tuberos, neural spine, occupying the entire central portion of the arch, while posteriorly on the under side of the centrum a feebly pronounced hypapophysis is seen. The odontoid apophysis is small and short as compared with other features of this vertebra, a fact no doubt due to the lack of depth in the atlas. At either side of the centrum we observe a delicate and vertical spicula of bone, which completely arches over the vertebral vessels, constituting the last remnants of the lateral canal at this extremity of the column. This condition is often met with among the *Anatidæ* in the axis vertebra of those birds.

The postzygapophyses are directed backwards and outwards, and are very powerfully developed, more so than in any of the first nine or ten vertebræ of this portion of the column. The facets they bear for articulation with the extremities of the prezygapophyses of the third segment are at their under side about the middle.

On the *third* and *fourth* vertebræ we also find a low neural spine placed at the centre of either bone, while the hypapophysis is becoming reduced in these segments, to disappear entirely in the fifth vertebra. These vertebræ, as in so many of the class, have their zygapophysial processes joined by a spanning lamina of bone, which in either case, and on either side, is pierced near its middle by a small elliptical foramen, of the greater size in the fourth vertebra.

The lateral canals occupy rather more than the anterior halves of the sides of the centra, and the processes that project from the under aspects of their free margins behind are short, and each is separated by a considerable interval from its fellow of the opposite side. This great inferior width of the cervical vertebra is a characteristic feature of these segments in *Geococcyx*,

and is well-sustained throughout the series, until we come to the free rib-bearing ones, when a gradual contraction takes place as we pass into the dorsal region. But even here the segments are comparatively broader in their transverse diameters than we often find them.

In the *fifth vertebra* the neural spine is placed further forwards on the bone, but is very small; it is absent in the *sixth*, or only faintly indicated, and it does not appear in the series again until we find it as a pronounced crest on the fifteenth segment. Sometimes, however, a low, tuberos elevation marks its site in the few ultimate cervicals.

Prezygapophyses in the fifth vertebra stand almost directly outwards, while the postzygapophyses very prominently point to the rear. Little modification takes place in the former of these processes as we examine the succeeding vertebræ, their general direction remaining about the same, but the articular facets they bear face more and more towards the median plane as we proceed backwards. With the postzygapophyses, however, the case is otherwise, for as we descend the cervical series we find these become gradually shorter and stouter, with a wider divergence, while their facets, from facing downwards and outwards, come to look almost directly downwards.

We find strongly marked metapophyses surmounting the bases of the postzygapophyses in the sixth to the ninth cervical vertebræ inclusive; after that they disappear, and are but feebly reproduced in the dorsals, where they occur on the superior aspects of the ends of the transverse processes.

On the fifth cervical vertebra the lateral canal is at its forward part, appropriating about the anterior moiety of the entire centrum. Its outer wall may show a slight perforation, while the parapophyses which project from it behind are on either side a short and needle-like spine. As we pass down the series this perforation becomes larger and larger, until in the tenth vertebra it has broken through the hinder free margin of the lateral canal and disappeared, leaving in the segment only a shorter passage, and a deep concave notch indicating its site. *Pari passu* with this change, the parapophyses and pleuropophyses pass through the usual evolution in that direction, to result in the perfect and free pair of ribs found in the thirteenth

vertebra. Faint beginnings of a carotid canal are also seen in the fifth vertebra, in the presence of a shallow excavation at the anterior end of the under side of segment. This becomes better and better marked to include the tenth vertebra, where this canal is moderately well protected by lateral walls, but in none of the series does it become a closed passage as in some other birds. In the eleventh vertebra its place is taken by a strong, single, and median hypapophysis.

This latter feature becomes faintly tricornuate in the twelfth vertebra; markedly so in the next segment; the three prongs springing from a common pedicle in the fourteenth; which pedicle is lengthened in the fifteenth; still longer but without terminal prongs in the sixteenth vertebra; to be entirely absent in the succeeding segment, and the rest of the column.

In the atlas the neural canal is capacious and transversely elliptical. From this vertebra it gradually changes its form and contracts in calibre, until in the fifth vertebra we find it nearly cylindrical in shape, and much reduced in capacity.

Passing down the series it gradually changes for a second time, so that in the eleventh vertebra it is again found to be large and transversely elliptical. This form it retains through the dorsal series, though once more reduced in calibre. In the tail vertebrae it is at first triangular with apex above, to become a vertical slit as it enters the pygostyle.

The fifteenth, sixteenth, seventeenth, and eighteenth vertebrae of the column in *Geococcyx* support ribs that meet to articulate with costal ribs below (Plate VIII. fig. 7). These ribs are broad above, but become more and more rod-like as they near their hæmapophysial articulations. The first three pair of the series bear large epipleural processes, which are always ankylosed to the rib upon which they appear. These three also have costal ribs connecting them with the sternum; this I believe to be the smallest number of the latter present in any living bird, *i.e.*, only three hæmapophyses articulating with either costal border of the sternum. The last pair of ribs, or those coming from the eighteenth vertebra, never have epipleural processes, and their costal ribs do not reach the sternum (fig. 7).

With respect to the four vertebrae that own these ribs, we find that they present all the characters of the dorsals as found

among Aves generally. The neural spines are lofty and quadrilateral in outline, each having its superior rim capped off with a vertically flattened tablet of bone. The diapophyses are rather broad, and project directly outwards from the sides of the vertebræ, having the ribs articulating with them and the centra in the usual way. Very close interlocking is evidenced among these four dorsal segments, and the post- and prezygapophyses are no longer than is necessary to afford the proper amount of surface for their respective articular facets. Anteriorly, these face upwards and inwards, precisely the reverse being the case with those found on the postzygapophyses.

So far as we have examined the vertebral column, the articulation which obtains among the centra is upon the *heterocoelous* plan, i.e., the anterior facet is concave from side to side, convex from above, downward, precisely the reverse condition being present in the posterior facet. All these vertebræ, as well as both kinds of ribs, are eminently pneumatic, groups of foramina occurring at the usual sites in these bones.

The Pelvis (Plate VIII. figs. 9, 10 and 11).—From its singularly unique form the pelvis of *Geococcyx* has attracted the attention of a number of anatomists. Owen speaks of the ilium as forming behind "a prominent ridge in most birds, which generally overhangs the outer surface; in *Geococcyx*, to a remarkable extent, like a wide pent-house, producing a deep concavity in the outer and back part of the ilium, where it coalesces with the ischium."¹

Marsh, in his classical work upon the *Odontornithes*, again calls attention to the same thing, and points out other particulars in connection with it, making admirable comparisons with the pelves of *Reptilia*, *Tinamus*, and other forms.²

Strange to relate, the only other living American bird, so far as I have examined, that possesses a pelvis anything like the one we find in *Geococcyx*, is the common sora rail (*Porzana carolina*).

¹ *Anat. of Verts.*, vol. ii. p. 34, Lond. 1866.

² Marsh, O. C., *Odontornithes*, pp. 70–73, figs. 16–20, Washington Government Printing Office, 1880. There certainly can be nothing that advances our knowledge of the exact origin of birds more certainly than the constant comparison of recent forms with the material palæontology has thus far been enabled to supply us,—not a great deal as yet. Professor Marsh never seems to allow such an opportunity to escape him.

This bird not only has the ilia forming the peculiar outward-curling crests behind, but has also the propubis well marked, and identically the same style assumed by the anterior portions of the ilia, *i.e.*, a deeply concave inner margin, with the sacral crista mounting above it, and not coming in contact with the same.

Viewing the pelvis of *Geococcyx* from above, we are to notice the condition just alluded to (fig. 10), as well as the raised, anterior emarginations of these ilia, with the processes that project from their middle points. As already hinted, the ilio-neural canals are here open grooves, and the neural crest of the sacrum stands between them as a lofty dividing wall, with much thickened superior border. This latter is distinctly marked for the entire length of the sacrum, otherwise the individualisation of the vertebræ composing this part of the bone is not very distinct, as few foramina are to be found between their diapophyses, until we reach the last one, where regularly occurs a large pair, throwing the ultimate uro-sacral into bold relief (fig. 10).

Owing to the spreading of the ilia, both laterally and behind, the superficies of the postacetabular, far exceeds the preacetabular, and these iliac bones are much tilted up posteriorly.

Upon the lateral aspect of this pelvis (fig. 9) we not only gain a better view of the largely developed propubis, and the strangely formed hinder portion of the ilium, but we are also enabled to get a glimpse of the rather small subcircular ischiac foramen, with the reniform antitrochanter in front of it. This latter faces almost directly forwards, and only slightly downwards, and less so outwards. Beyond this again is the acetabulum, with the circular perforation at its base, the postero-superior arc of which merges with the periphery of the outer cotyloid ring at the base of the antitrochanter, while directly opposite this point the arcs of these two circles are far apart, and an excavation occupies the intervening space. This grows less, of course, as we proceed either way towards the base of the antitrochanter, where, as I have said, the inner and outer rings are tangent to each other.

The elliptical *obturator foramen* occupies its usual position, and so close together are the post pubis and ischium that an exceedingly narrow strait leads from this vacuity into the

obturator space, a long narrow interval between the last two mentioned bones. At the centre of the triangular area among these three apertures at the side of this pelvis, is found a group of small pneumatic foramina which assist in admitting the air into the substance of this light and thoroughly aerated bone.

The Caudal Vertebrae and Pygostyle.—As already stated above, the caudal vertebrae are five in number (Plate IX. fig. 17). They are chiefly noted for their high and prominent neural spines; the two loftiest being seen in the third and fourth vertebrae. The diapophyses grow longer and more spreading as we proceed in the direction of the pygostyle, the last segment possessing them longer than any of the others. We find in the third caudal vertebra a small anchylosed chevron bone, which slightly overlaps the bone in front of it. This apophysis is very strongly developed in the last two vertebrae, where it is also anchylosed to the centra, is bifid, and hooks well forward to overlap the preceding centrum in either case. Each one of these bones is pierced by pneumatic foramina in a number of places, as is also the terminal coccygeal vomer.

This latter bone has an irregular oblong figure, with its posterior margin considerably thickened, the others being cultrate. The neural canal is continued into it for some little distance, its passage being denoted on the sides of the bone by a longitudinal smooth elevation, which gradually tapers away to the postero-superior angle.

Of the Sternum and Pectoral Arch.—The sternum of *Geococcyx* is a thoroughly pneumatic bone, but air does not gain access to any of the shoulder-girdle elements.

In the case of the former, foramina are chiefly found in the concavities among the hæmapophysial facets on the costal borders. A few scattered ones may be seen in the median line upon the dorsal surface. The number of these latter vary in different specimens.

The "Road Runner" has a two-notched sternum, which gives rise to a pair of flaring xiphoidal processes on either side (figs. 7, 16). Its carina is fairly well developed and moderately deep only. It extends the entire length of the bone, and is marked upon the upper side of its projecting carinal angle by a roughened facet for articulation with the hypocleidium of the furculum.

Osseous welts are raised upon its sides to facilitate muscular attachment, and these in some specimens, extend on to the ventral aspect of the body (fig. 16). The inferior border of the keel is somewhat thickened.

In front of the sternum a peg-like manubrium projects out, the lower margin of which is longitudinally marked by a sharpened crest (fig. 7). Below this, the perpendicular anterior border of the keel is vertically concave, and this inferior manubrial crest is carried into the excavation as a median raised line.

Either costal border is very short, having but three facets upon it, and these are usually close together. In front of them, on either side, a prominent costal process is reared, constituting one of the most striking features in this part of the skeleton of *Geococcyx* (fig. 7).

The thoracic aspect of the sternum is very much concave, the ventral side being correspondingly convex. Here on this latter we notice well-marked muscular lines, one on either side, commencing at the outer termination of a coracoidal groove, and running backwards to a point about opposite the middle of the keel.

The coracoidal grooves do not meet at the manubrial base in the median line, and each one is characterised as being a deep transverse notch, with upper and lower lips of projecting bone and extending laterally only so far as the inner or anterior limit of the base of the corresponding costal process.

With respect to the *pectoral arch*, I find a *coracoid* to be, comparatively speaking, an unusually long bone; its sternal or lower border extends beyond the facet proper, in order to fit into the coracoidal groove of the sternum. This end of the coracoid is not as much expanded as we find it in some birds, but, on the other hand, like many of the class, its outer angle is produced and bent upwards as a projecting process.

The shaft is long and cylindrical, being marked down its posterior and lateral aspects by muscular lines.

At the superior, or really anterior extremity of this bone, we find several noteworthy and interesting characters (fig. 5).

Its scapular process is very long, and compressed from side to side. This apophysis reaches forwards, and by its slightly dilated extremity articulates with a vertically concave notch in the lower part of the head of the corresponding clavicle.

Another meeting between these two bones takes place above, and this is affected by the summit of the coracoid curving inwards towards the median plane, to articulate with a considerable facet found at the highest point of the clavicular head.

These two articulations between the furculum and the coracoid completely close the tendinal canal, even without the assistance of the scapular behind, though this latter bone materially aids in increasing the actual length of this tendinal passage, by closing up the posterior gap.

If we turn to the dotted outline of the *cs furculum*, shown in figure 6, it will be noticed that it has a form about intermediate between the usual U and V shapes of the bone. Regarding it from a lateral aspect, as shown in the preceding figure, the actual form of one of its transversely compressed heads can be better appreciated, as well as its method of articulation with the other bones of the girdle (fig. 5).

Below it is flattened in the antero-posterior direction, and terminates in an elongated hypocleidium. This latter articulates when the arch is *in situ* with the carinal angle of the sternum, in the manner described in a foregoing paragraph.

A *scapula* assists to form the glenoid cavity in the usual way, contributing about half the surface to that humeral socket. Its clavicular process reaches far forwards, to make an extensive articulation with the head of the furculum, when the bones are in the position they assume in life. It also rests further forwards upon the scapular process of the coracoid than is usually seen among birds (fig. 5). Sometimes we find the posterior third of the long, narrow blade of this bone bent down more abruptly than in the specimen I have figured, and its end is always rounded off, rather than being truncated, as is commonly the condition in Aves.

At the outer and back part of the shoulder-joint in the adult *Geococcyx*, occurs usually a very minute sesamoid, known as the *os humero scapulare*, and I am led to believe that small sesamoids may yet be found in other of the tendons of the pectoral extremity in this region.

Of the Appendicular Skeleton—The Pectoral Limb (I late VIII. figs. 12-15).—Pneumaticity is extended only to the bone of the

brachium in this limb, the hollow shafts of the other long bones being charged with medullary substance.

The humeral shaft is much bowed, and in such a manner as to be convex along its radial border and concave upon the opposite side, which concavity is more apparent owing to the prominence of the ulnar crest, and the peculiar projection of the distal extremity in the continuity of this curve (figs. 12, 14).

In form the shaft is nearly cylindrical, and almost entirely devoid of muscular lines.

At the proximal end, a well-marked valley occurs between the ulnar crest and the spindleform humeral head. The former has barely any pneumatic fossa at its base, the circular foramen there found being nearly flush with the general surface of the bone. On the opposite aspect we find a short though prominent radial crest, which makes no pretence to extend its lamelliform plate down the shaft, as we often find to be the case in birds.

The distal extremity of this bone presents for examination the usual oblique and ulnar tubercle, while, as already alluded to, the ulnar condyle of this end is much produced and very prominent (figs. 12, 14).

The anconeal aspect immediately above the trochlea is flat and smooth, the opposite side showing a broad, shallow groove for the guidance of tendons to the antibrachium. A fairly well-developed "ectocondyloid tubercle" is seen at its usual site, on the radial border of the shaft just above the oblique trochlea.

Following the example of the humerus, we find the comparatively short *radius* and *ulna* very much bowed along the continuity of their shafts. This gives rise to a broad spindle-shaped interosseous space, the two bones only coming in contact at their distal and proximal extremities, when articulated (fig. 13).

The *radius* is not nearly so much bent as the other bone of the antibrachium, and presents nothing peculiar about it. On the other hand, the *ulna*, with its greatly curved shaft, its prominent row of secondary papillæ, and its well-developed olecranon, is quite a striking bone beside it.

Composing the elements of the carpus, the two usual free segments are seen; of these the *radiale* has pretty much the

same form as it assumes among birds generally, while the *ulnare* takes on an entirely different shape. It does not develop the two limbs or processes that straddle the proximal extremity of the carpo-metacarpus, when the bones are *in situ*, as in the vast majority of the class, but is simply a bar of bone, with one end enlarged, and bearing at its summit an articular facet for the ulna.

The *carpo-metacarpus* is chiefly interesting for its peculiarly formed mid-metacarpal. This is uncommonly broad at its proximal end, and curiously twisted, as it descends to ankylose with the lower end of the index metacarpal, or main shaft of this compound bone. So far as I have been enabled to discover, the phalanx of pollex-digit does not bear a terminal claw, and the bone has the usual form as seen in most Aves. Nothing of note distinguishes the two phalanges of the index digit, while the small phalanx of the last finger develops, at the middle point of its hinder margin, a curious little upturned spur (Plate VIII. fig. 13).

Of the Pelvic Limb (Plate IX. figs. 18-27).—As in the pectoral extremity, the proximal long bone of this limb, the *femur*, is the only one in it that enjoys a pneumatic condition. The site of the foramen that admits the air to its hollow shaft is, however, quite unique, being upon the posterior aspect of the bone, between the trochanter and head, instead of on the anterior side, as usual, below the trochanter.

This latter feature is not elevated above the articular surface at the summit, and the semi-globular head is, comparatively speaking, rather small. A shallow excavation upon its upper side marks the usual point for the insertion of the round ligament.

The sub-cylindrical shaft faintly showing the muscular lines, is considerably bent to the front, as shown in fig. 19.

At its distal extremity in front, the rotular channel is well marked, the condylar ridges bounding it being about parallel to each other (fig. 18).

The outer and larger condyle of the two is at the same time the lower, and the fibular cleft that marks its posterior aspect, is very wide and deeply sculpt, being rather more to the outer side than is usual (fig. 20).

Above these condyles, behind, the popliteal fossa is but moderately excavated, and a straight transverse line bounding it below divides it from the general trochlear surface.

We find in the next segment of this limb, the *tibio-tarsus* with a subcylindrical shaft below its fibular ridge, that is slightly bent so as to be in the vertical line, somewhat convex anteriorly (fig. 22). The bending here though is not nearly so great as we found it to be in the humerus and femur, or, to make the comparison more exact, in the ulna.

The cnemial crest of this leg-bone is but little raised above the undulating articular surface of its summit, while the pro- and ectocnemial ridges, that develop below it, are not peculiar (figs. 21-23). Their planes are at right angles to each other, that of the latter having its surface facing directly to the front. Neither is produced for any distance down the shaft of the bone, but terminates rather abruptly upon it; the pro-cnemial ridge at a point about opposite the superior end of the fibular ridge on the other side of the shaft (fig. 21).

At the distal extremity of the tibio-tarsus the planes of the condyles are nearly parallel to each other, and these trochlear eminences are strikingly close together in *Geococcyx*.

The intercondyloid fossa is deeply excavated in front, to become suddenly much shallower behind, as well as somewhat narrower. Upon lateral view, it will be seen that the general outline of either of the condyles is more circular than we usually find it in others of the class, where a reniform pattern prevails (fig. 22).

Just above the condyles, on the anterior aspect, the vertical tendinal channel is spanned by the usual little, oblique bridge of bone, and this is supplemented in life by a longer ligamentous one placed in front of it.

The *fibula* has a large head, which is produced backwards beyond its shaft. This latter makes a close ligamentous articulation with the fibular ridge of the tibio-tarsus, and at some little distance below it merges into its shaft, to become almost indistinguishably fused with it (figs. 21-23).

A well-developed, subcordate *patella*, with its apex directed below, is found in the usual tendon in *Geococcyx*.

It will be seen by referring to figures 24 and 26 that the

tarso-metatarsus of the Road Runner is a longer bone perhaps, than we would be led to expect from the other long bones of this limb.

Its summit presents for examination the two concavities for the condyles of the tibio-tarsus, separated by the mid-tubercle. Behind this we find a short hypo-tarsus, showing two vertical grooves at its back, and two vertical perforations through it, as shown in fig. 25.

The sides and front of this bone are flat, the latter for its proximal half being longitudinally grooved, deepest above, gradually becoming shallower as it descends. Posteriorly it is likewise grooved in a somewhat similar way; but here the outer wall of the groove is raised as a sharp longitudinal crest, best marked at the middle third of the shaft, and gradually subsiding towards the extremities.

At the distal end we note the three usual trochleæ for the basal joints of the toes; figure 27, however, shows how, in this zygodactyle bird, the outer one of these is extended to the rear, in such a manner as to allow the fourth toe to articulate in that direction (figs. 26 and 27).

Of these trochleæ the middle one is much the largest and is placed the lowest down; it is the only one of the three that shows the distinct median groove. The trochlea for the fourth toe is much elevated, while the inner one holds about a mid-position in this respect.

A well-developed accessory metatarsal, slung by ligament in the usual way, is found between the shaft and the basal joint of the hallux (fig. 26). The perforating foramen for the passage of the anterior tibial artery is small and inconspicuous, being at the same time quite low down on the shaft.

The joints of these podal digits are harmoniously proportioned, both as regards size and comparative length, and beyond what can be easily studied in my drawing of them, and their typical zygodactylism, they offer nothing of particular note.

Before reducing my specimens to skeletons, I failed to make any special examinations as to the condition of the ossifications of the columella auris in the adult *Geococcyx*; I find, however, among other normal ossifications in this type, some twelve or thirteen sclerotal plates in either eye, overlapping each other in

a somewhat irregular manner. The rings of the trachea also ossify as in other birds, as well as the plate of the superior larynx. Some of the tendons of the pelvic limb in old birds are also converted into bone, and small sesamoids may be found about the proximal extremities of the basal joints in the soles of the feet.

During the preparation of this memoir several more Pacific Coast specimens of this form have come into my hands; among others I am indebted to Mr W. Otto Emerson of Haywards, California, for the present of a very fine male bird. I also have a young one, just leaving the nest, but my further examination of this material reveals to me nothing in the skeleton of the adult to be added to the above detailed description of my type specimen from Santa Barbara, California, from which I made all the drawings in the accompanying illustrations in the Plates.

EXPLANATION OF PLATES VII., VIII., IX.

[The figures are all life size and from the same specimen.]

Fig. 1. Left lateral view of skull and mandible of *Geococcyx californianus*, ad. ♂.

Fig. 2. The mandible seen from above.

Fig. 3. The skull from superior aspect; mandible removed.

Fig. 4. The skull seen upon under view; mandible removed.

Fig. 5. Right half of the pectoral arch seen from the inner side; the coracoid, furculum, and scapula *in situ*.

Fig. 6. *Os furculum* in dotted outline; viewed from behind.

Fig. 7. Left lateral view of dorsal vertebrae, ribs and sternum; the bones all in their natural positions.

Fig. 8. The hyoid arches seen upon superior view; the thin glossohyal is dotted to represent cartilage.

Fig. 9. Left lateral view of pelvis.

Fig. 10. Superior aspect of pelvis.

Fig. 11. Pelvis seen upon direct posterior view.

Fig. 12. Right humerus, palmar aspect.

Fig. 13. Palmar aspect of radius and ulna, and the bones of the carpus and manus; same limb.

Fig. 14. Right humerus, anconeal aspect.

Fig. 15. Right humerus, radial aspect.

- Fig. 16. The sternum seen upon its pectoral aspect.
- Fig. 17. Caudal vertebræ and pygostyle, seen from the right side.
- Fig. 18. Anterior view of left femur.
- Fig. 19. Inner view of left femur.
- Fig. 20. Posterior view of left femur.
- Fig. 21. Left tibio-tarsus and fibula, seen from in front.
- Fig. 22. Left tibio-tarsus and fibula, their outer aspects.
- Fig. 23. The summits of the left fibula and tibio-tarsus.
- Fig. 24. Anterior view of the left tarso-metatarsus.
- Fig. 25. The summit of the left tarso-metatarsus.
- Fig. 26. Right lateral view of the skeleton of the left foot of *Geococcyx*, including the tarso-metatarsus.
- Fig. 27. The distal extremity of the left tarso-metatarsus, showing the trochleæ as seen directly from beneath.

ON THE RELATIONSHIP OF UREA FORMATION
TO BILE SECRETION: AN EXPERIMENTAL
RESEARCH. By D. NOËL-PATON, M.D., B.Sc., *Biol.*
Fellow of the Univ. of Edin.

(From the Physiological Laboratory of the University of Edinburgh.)

(Continued from page 124.)

PART II.—EXPERIMENTAL.

No direct series of experiments upon this subject has been made, but many well-known physiological facts strongly indicate the existence of such a relationship. In the first place, in the starving animal, the excretion of urea and of bile (Bidder and Schmidt) falls, and to the last days of life persists in small amounts. In the second place, after a meal both urea excretion and bile secretion rise, and reach their maximum some hours after food is taken. Lastly, the influence of different diets on the urea excretion on the one hand, and the bile formation on the other, is of interest: while proteids cause a marked increase in both, fats have no stimulating effect upon either process.

Instead of following the lines suggested by these past observations, I have employed, as before mentioned, another, and I believe more satisfactory method—that of studying the influence on the urea excretion in dogs in a state of nitrogenous balance (*stickstoffgleichgewicht*) of certain drugs, which powerfully stimulate bile secretion.

My earlier experiments were made upon men, but the results obtained, owing to the many disturbing causes which could not be excluded, were so unsatisfactory, that after two months' work, this mode of experiment was abandoned, and the observations were repeated in dogs.

For all the experiments here recorded, with the exception of two, dogs were employed. And I believe that the use of these

animals renders my results of more value, as it was upon dogs that Professor Rutherford conducted his series of experiments upon bile secretion; so that we may in every case safely conclude that under the administration of the drug the secretion of bile really was stimulated.

Mode of Experiment.

Large female dogs were selected, weighing about 13 kilos. Female dogs were chosen, because from their mode of micturition there is less chance of a loss of urine occurring; and, when catheterisation is required, it is more easily and safely performed than upon the male.

The dog was kept in a cage of 40 inches square by 38 inches in height.

The floor was of smooth zinc, and sloped from all sides to a hole in the centre, under which was placed the vessel in which the urine was collected.

Across one side of the cage was stretched a narrow board, on which the dog slept and fed, but upon which it rarely micturated.

The floor of the cage was kept scrupulously clean, and was frequently washed with a solution of permanganate of potash. The faeces were always cleared away as soon after they were passed as possible.

I am well aware that my method of collecting the urine allows of a certain loss, but that this is a fixed percentage quantity is shown by the very uniform daily excretion of urea which my analyses indicate. Using this method, I have been able, by carefully regulating the diet, to approach almost as near to a daily uniform excretion of urea as Salkowski, Virchow, Wolfsohn, or other observers who have employed catheterisation, or who have educated their dogs to micturate into a vessel held beneath them (Wolfsohn). In some of my experiments I have observed a tendency to a bi-diurnal type of urinary excretion (see Exp. IV.), a small amount of urine being passed on one day, followed next day by a more copious quantity. But if a mean be taken for these two days, it corresponds very exactly with the normal daily excretion.

The urine was collected at ten o'clock each morning; the cage was then cleaned, and the dog fed.

The urine was measured, and set to filter. The specific gravity was taken, and the urea and uric acid at once estimated.

Diet.

The diet consisted of oatmeal porridge with milk. On this food the dogs remained healthy for long periods, even when confined to the circumscribed limits of their cage. This diet caused a firm well-formed fecal dejection daily, a matter of no small importance, as the urine was thus kept free for admixture with feces.

The urine too was large in amount and of low specific gravity, so that the dilution usually required in observations on dogs' urine was thus rendered unnecessary.

Methods of Analysis.

I. *Urea*.—For the quantitative estimation of the urea I have employed the hypobromite method of Hüfner.

In preferring this process to the more commonly adopted method of Liebig, I feel that I have exposed myself to adverse criticism. But a careful perusal of the very extensive and scattered literature upon the subject, and a series of experiments undertaken by myself, has fully convinced me that, for such a research, this method has advantages over all others. It may be rendered more accurate than Liebig's method, and it has this great advantage, that the presence in the urine of the drugs administered does not interfere with the results.

The solutions employed were the following:—

1st, Solution of sodic hydrate prepared by dissolving 230 grms. of caustic soda in 500 c.cs. of water.

2nd, Bromine.

These were mixed in the proportion of 1 in 10, and the hypobromite solution was freshly prepared each morning.

The apparatus of Dupré was adopted, and was first carefully tested with standard solution of urea, in order to determine the percentage loss of nitrogen. This was found to correspond

very closely to that observed by Leconte, Mehu, Foster, and Russel and West.

Corrections were made for temperature and pressure according to the formula given by Hüfner (*Journal of Prakt. Chemie*, N. F. Bd. III. p. 11, 1871).

V = volume of gas at 0° C. and 760 mm.

V' = the volume read off.

B = barometric pressure in mms.

W = tension of aqueous vapour at temp. at which decomposition occurs.

T = temp. in °C.

The formula is
$$V = \frac{V'(B - W)}{760 (1 \times 0.00366 T)}.$$

Great care was taken to carry out the decomposition at a low temperature, and time was always allowed for the gas throughout the apparatus to become of a uniform temperature before and after the decomposition occurred.

II. *Uric Acid*.—For the estimation of the uric acid I have selected the method recently devised by Professor Haycraft, because it appears to me to combine, more than any other, the two qualities of accuracy and rapidity. I have tried Heintz's, Cook's, and Pavy's, and have failed to get results so nearly accurate; while Salkowski's very admirable method is much too tedious for every day analysis.

Through the kindness of Prof. Haycraft I have been enabled to use this process throughout all my experiments, although his paper on the subject has only recently appeared (*Brit. Med. Journ.*, vol. ii. 1885, p. 1100).

EXPERIMENTS.

I. SALICYLATE OF SODA.

According to Professor Rutherford's experiments 62, 66, 67, 69, 70A and 73A and 74A, salicylate of soda occupies perhaps the first position among the cholagogues in its influence on the bile secretion. Professor Rutherford says of it—"Indeed this substance is a certain hepatic stimulant, never failing when

placed in the duodenum to excite the liver within half an hour."

Only a few observations on the influence of salicylate of soda on the urinary constituents have as yet been recorded.

In 1876 two papers on the subject appeared, one by Chr. Bohr bei Panum in *Hospitals Tidende*, 2, iii. p. 129, and the other by Solomon Wolfsohn (*Ueber die Wirkung der Salicylsäure and des Salicylsauren Natron auf den Stoffwechsel*).

Bohr's paper I have been unable to procure. But, from the account of his results given at p. 173 of vol. vi. of Hermann's *Handbuch der Physiologie*, it appears that the dogs upon which his observations were made were allowed to drink what water they pleased, and he connects the rise in the urea with the increased imbibition of water, which is supposed to have increased the tissue metabolism. His results cannot therefore be considered of any value.

Wolfsohn gives six experiments, two upon salicylic acid and four upon salicylate of soda. In five of his experiments, the drug was given by the mouth, and in one the salicylate of soda was hypodermically administered. In all his experiments he was able to demonstrate a well-marked increase in the total nitrogen and in the urea excreted, and this increase in his experiments was best marked on the days following the administration of the drug.

Since he does not state the weight of the dog employed, and since the diets used by him differ from that employed by me, it is impossible to compare our results in detail.

Carl Virchow (*Ztsch. f. Physiol. Chem.*, vol. vi. p. 78) gives an experiment on the influence of salicylate of soda on the total nitrogen of the urine. This was performed in Professor Salkowski's laboratory on a female dog, weighing between 22 and 24 kilos., and fed upon 500 grms. of flesh, 75 grms. of bacon, and 200 grms. of water daily. The urine was collected by catheterisation. The nitrogenous excretion before the experiment was anything but constant; nevertheless his general results correspond closely with my own.

Although the action of the benzoates upon the excretion of uric acid has, on account of their connection with the production of hippuric acid, attracted considerable attention, I am not aware

of any observations upon the influence of their allies, the salicylates, upon the urinary constituents. Sée, indeed, in a paper published in the *Bul. de l'Acad. Med.*, 1877, p. 704, states that in gravel and gout the uric acid excreted is increased under the administration of salicylate of soda, while in health these drugs have no influence whatever either upon the urea or the uric acid. He states that in acute gout he has seen the uric acid rise from 0.30 grms. per 1000 c.cs. to 3.10 grms. per 1000 c.cs. But, as Garrod has shown, a similar rise occurs in all cases of acute gout towards the termination of the attack; so little value can be placed on Sée's observations. All the more are they unworthy of attention, as he does not record the experiments upon which they are founded.

The action of this drug, which is now so largely used in the treatment of rheumatism and gout, and which promises to become one of our most valuable remedies in diabetes, appeared to me to deserve special attention. I have accordingly devoted six experiments to its investigation, four of which I now record.

Exp. I. and II.

For these two experiments a man, aged 56, was employed; his daily exercise was fixed, and his diet was daily, without any variation, the following:—

Breakfast.—Bread, 4 oz; tea, 1 pint.

Dinner.—Broth, 1½ pints; beef, 4 oz.

Supper.—Porridge, 1½ pints; milk, ½ pint.

He took little or no water—never more than a tea-cupful in the twenty-four hours.

The daily excretion of urea never became very constant, but the influence of salicylate of soda is seen in the accompanying table and abstract, and in fig. 1 (p. 274.)

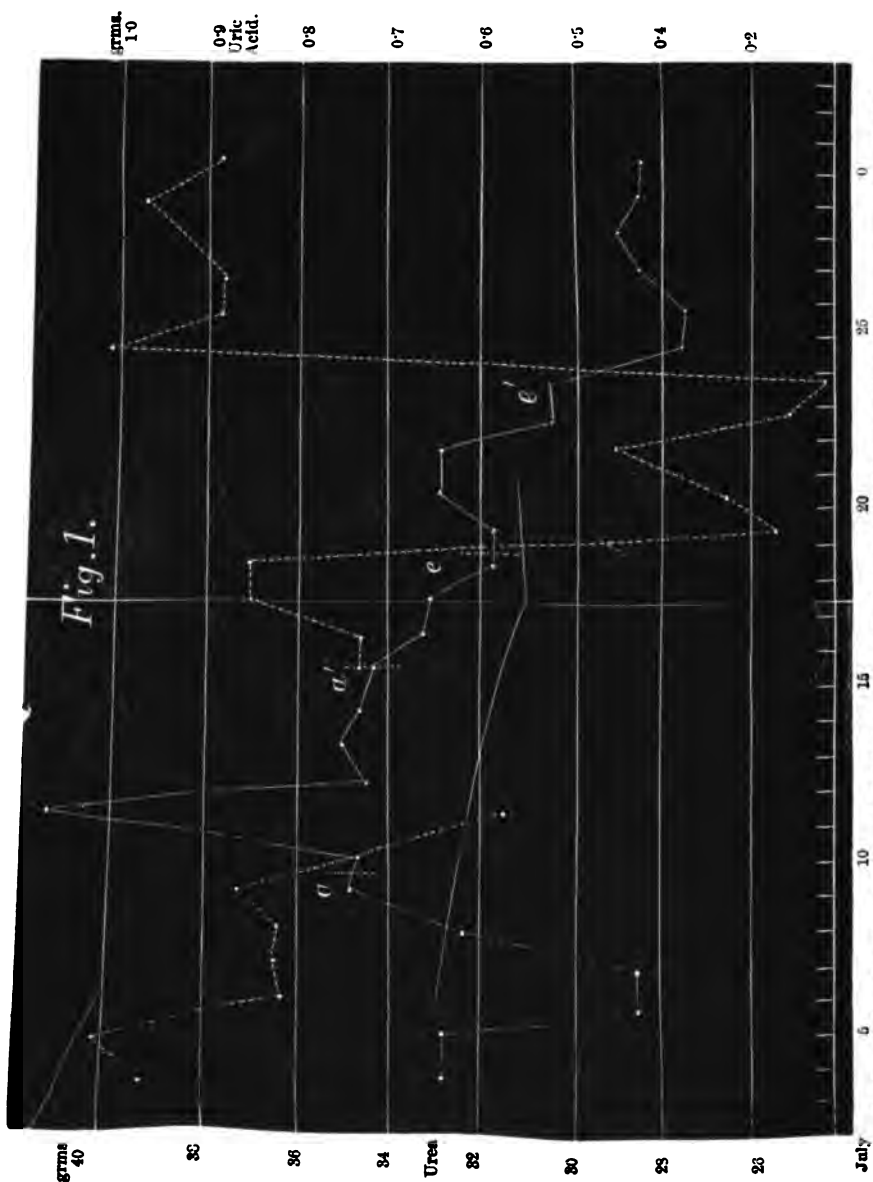
Exp. I. and II.¹

Date.	Urine in c.ca.	Sp. G.	Urea in Grms.	Uric Acid in Grms.	Remarks.
3·7·84	2215·2	1014	33·671	0·968	Weight of man—62·1 kilos. Diet—(as above).
4	1918·2	1015	32·058	1·037	
5	2158·4	1013	29·344	0·811	
6	1618·8	1015	27·681	0·833	
7	2556·0	1012	32·205	0·823	{ 6·6 grms. sodæ salicylatis in 24 hours—0·106 grm. per kilo. of body weight. Reaction with FeCl ₃
8	1646·3	1018	34·901	0·874	
9	1646·3	1016	34·572	0·663	
10	2414·0	1018	41·521	0·567	
11	1760·8	1019	34·335	...	" "
12	2101·6	1016	35·096	...	" "
13	1959·6	1016	34·489	...	" "
14	1618·8	1017	34·156	0·720	Faint " "
15	2385·6	1013	33·898	0·701	" " "
16	2272·0	1013	33·171	0·800	" " "
17	2158·4	1014	31·982	0·850	{ 6·6 grms. sodæ salicyl. in 24 hours—0·106 grm. per kilo. Reaction with FeCl ₃
18	2101·6	1013	31·982	0·281	
19	2442·4	1016	32·349	0·321	
20	1988·0	1014	32·349	0·441	
21	1533·6	1013	30·590	0·257	" "
22	2044·8	1015	30·590	0·206	" "
23	1817·6	1016	27·860	1·001	" "
24	2585·6	1013	27·860	1·119	
25	1902·8	1015	28·351	0·679	
26	2158·4	1013	28·922	...	
27	1931·2	1014	28·870	0·984	
28	1902·8	1013	28·870	0·894	
29	1874·4	1012	24·742	...	

Average daily Excretion of Water and Urea under Salicylate of Soda:—

	Water.	Urea.
	c.ca.	grms.
Before Exp. I.,	1930	30·62
During administration of drug,	2012	34·72
Between Exp. I. and II.,	2108	33·77
During second administration of drug,	2016	31·30
After Exp. II.,	2027	28·40
Before and after Exp. I. and II.,	2003	29·51
During administration of drug in Exp. I. and II.,	2014	33·01
Percentage change in Water,	practically unaltered.	
" " Urea,	+ 11·89 c.	

¹ In this and all subsequent tables, the date refers to the day upon which the greater part of the urine was passed—not to the day on which it was collected. Thus the urine of 3·7·84, is the urine collected at 10 A.M. on the 4th July.



Exp. II. and II. — Excretion of Urea and of Uric Acid under Salicylate of Soda. 6.6 grms. given at *a*, urine gave reaction with FeCl_3 till *a'*; 6.0 grms. given at *e*, urine gave reaction with FeCl_3 till *e'*.

Average daily Excretion of Uric Acid in grms. under Salicylate of Soda :—

Exp. I.

Before.	With.	After.	Before and After.	With.
0·895	0·732	0·842	0·868	0·782

Percentage change = -15%.

Exp. II.

Before.	With.	After.	Before and After.	With.
0·767	0·303	0·931	0·849	0·303

Percentage change = -64·3%.

Haycraft's method was used in these, as in all future experiments, for the determination of the uric acid; and, as the presence of this drug in the urine might have interfered with the accuracy of the process, this possible source of error was excluded by the following experiment:—

Exp. IA.

The uric acid in a specimen of urine was by this method found to be 0·0221%. A large quantity of salicylate of soda was then added to another portion of the same urine, and upon testing the percentage of uric acid was found to be 0·0228%.

Therefore, salicylate of soda has no effect in the accuracy of this process.

Exp. III.

On the 27th January, salicylate of soda was given in 2 grm. doses, made into pills with a little mucilage, at 1 P.M., at 4 P.M., and at 6 P.M. There was no sickness, but next morning the dog appeared dull, though it took food greedily. 2 grms. were administered at 11 A.M. on the 28th, but the dog appeared so ill that the drug was discontinued. The effect of such large doses of salicylate of soda is shown in the table, abstract, and in fig. 2. The effect on the kidneys was marked. On the 29th the urine passed was of very high sp. gr., and contained a large amount of albumin, but no blood. The albuminuria persisted for three days. The drug had absolutely no influence upon the bowels.

Exp. III.

Date.	Urine in c.cs.	Sp. G.	Urea in grms.	Uric Acid in grms.	Bowels.	Remarks.
20-1-95	530	1013	7-260	0-148	moved	Weight of dog=13-6 kilos.
21	550	1012	7-370	0-126	"	Dist.
22	600	1013	7-880	0-132	"	Oatmeal as porridge 113 grms.
23	610	1013	7-320	0-140	"	Milk 320 c.cs.
24	470	1011	7-442	0-126	not moved	
25	600	1014	7-442	...	moved	
26	485	1014	7-394	0-125	not moved	
27	240	1017	4-100	0-064	"	6 grms. } 8 grms. sodæ salicyl. in 22 } hours.
28	0	moved	2 grms. } =0-6 grm. per kilo. weight } of dog.
29	1130	1026	32-192	0-265	not moved	Reaction of salicyl. with FeCl ₃ , marked albuminuria.
30	340	1019	9-900	0-102	"	Reaction of salicyl. with FeCl ₃ , trace of albuminuria.
31	300	1010	9-168	0-208	moved	Reaction of salicyl. with FeCl ₃ , trace of albuminuria.
1-2-95	745	1009	8-418	0-223	not moved	
2	urine lost	"	
3	570	1010	7-353	...	moved	
4	550	1010	18-222	0-154	"	
5	750	1013	18-222	0-192	"	

Average Daily Excretion of various Constituents under Salicylate of Soda :—

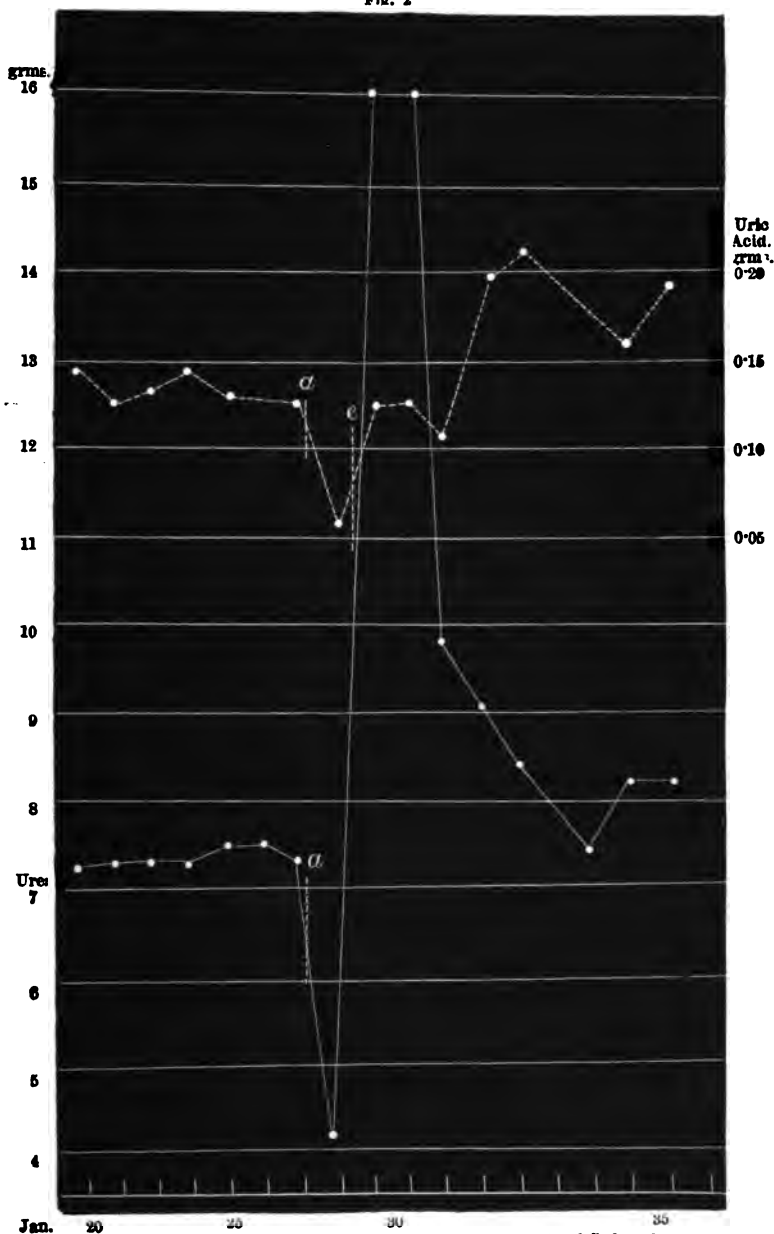
	Before Drug.	With Drug.	After Drug.	Before and After.	With.	Percentage Change in.
Water, in c.cs.	546	502	653	599	502	- 16-1%
Urea, in grms.	7-372	11-012	8-053	7-710	11-012	+ 42-7%
Uric Acid, ,,	0-132	0-126	0-189	0-160	0-126	- 21-3%

Exp. IV.

This is in every way a satisfactory experiment, and fully confirms all the results obtained in Experiment III. The dose was more moderate, and the kidneys were not so markedly affected. The diminution in the amount of uric acid is very well shown.

During this experiment the amount of urine daily passed varied considerably ; but on taking two days together and striking an average an almost constant daily excretion of urea was obtained. This bi-diurnal habit in regard to micturition was frequently well marked in this dog, but in no way interfered with the results of the experiments.

Fig. 2



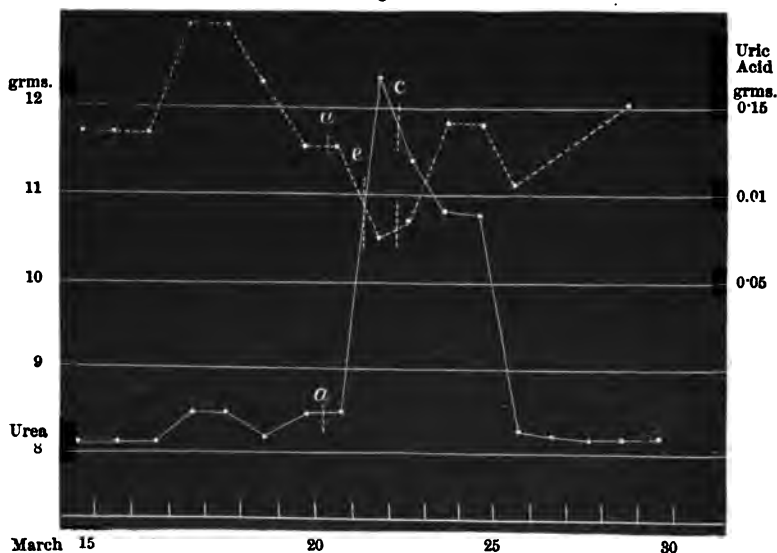
Exp. III.—Excretion of Urea and Uric Acid under Salicylate of Soda. 6 grms. given at *a*, and 2 grms. at *a*.

Exp. IV.

Date.	Urine n c.c.s.	Sp. G.	Urea in grms.	Uric Acid in grms.	Bowels.	Remarks.
14 '3 '85	{ 563		8.150	0.136	moved	Weight of dog=12.7 kilos.
15	{ 563		8.150	0.136	"	Diet—Porridge of 118 grms. oatmeal
16	{ 563		8.150	0.136	not moved	Milk, 820 c.cms.
17	{ 735		8.540	0.196	moved	
18	{ 735		8.840	0.196	not moved	
19	{ 830		8.200	0.166	"	
20	{ 595		8.538	0.129	"	
21	{ 595		8.538	0.129	moved	2 grms. salicylate of soda=0.16 grm. per kilo.
22	440		12.330	0.075	not moved	2 grms. " " 0.16 grm. per kilo.
23	500		11.400	0.085	"	3 grms. " " 0.23 grm.
24	{ 725		10.927	0.145	moved	Reaction with FeCl ₃ .
25	{ 725		10.927	0.145	"	" "
26	830		8.300	0.107	not moved	Slight " "
27						
28	{ 570		6.945			} Average daily excretion of urea =8.247 grms.
29	{ 570		6.945	0.153		
30	{ 645		9.550			
31	{ 645		9.550			

The brackets indicate that the figures given represent the average for period indicated.

Fig. 3.



Exp. IV.—Excretion of Urea and Uric Acid under Salicylate of Soda. 2 grms. given at *a*, 2 grms. at *e*, and 3 grms. at *c*.

Average Daily Excretion of various Constituents
under Salicylate of Soda.

	Before Drug.	With Drug.	After Drug.	Before and After.	With.	Percentage Change in.
Water, in c.cs.	691	482	695	693	482	- 30.4%
Urea, in grms.	8.353	11.393	8.258	8.305	11.393	+ 37.1%
Uric Acid, ,,	0.161	0.082	0.137	0.149	0.082	- 44.9%

Results.—With moderate doses of the drug, such as were given in Exp. I. and II., no influence on the amount of water excreted could be determined; with larger doses a well marked diminution in the amount of water occurred, and in Exp. III. distinct albuminuria was induced, showing that this drug has really an irritating action upon the kidneys. This observation fully bears out the results of clinical experience of its use, especially in scarlet fever, where it is undoubtedly an extremely dangerous remedy.

The urea was very markedly increased in spite of the diminution in the water.

The uric acid was very much diminished. This last is a point of great practical interest and importance, as it throws very direct light on the benefit derived from the use of the drug in gout. In the practice of M. Germain Sée it has entirely replaced the use of colchicum (*Year Book of Treatment for 1884*, p. 81).

How this diminution in the uric acid excretion is brought about it is difficult to understand. Obviously it is a diminished production and not merely a diminished excretion; for we have no great rise in the excretion upon discontinuing the drug.

Either salicylate of soda must cause a more complete metabolism of those bodies which yield both uric acid and urea, whereby they are entirely converted into the latter substance, or what is more probable, the production of salicyluric acid must interfere with the formation of uric acid.

To decide this point a quantitative examination of the uric acid and salicyluric acid under the influence of the drug would be necessary. Unfortunately, there is at present no method for

the accurate quantitative determination of the latter of these substances.

Bertagnini (*Annal. der Chem. und Pharmac.*, Feb. 1856) has shown that this salicyluric acid is produced by the synthesis of salicylic acid with glycol; while Horbaczewski states (*Wiener Akad. Sitzb.*, II. Abth., 1885, Mai) that he has prepared uric acid synthetically from glycol and urea. It is therefore highly probable that salicylic acid, by uniting with glycol to form salicyluric acid, prevents the production of uric acid. Dr Latham of Cambridge has already developed this view of the formation of uric acid in relationship to the treatment of gout by benzoates.

II. BENZOATE OF SODA.

Dr Rutherford, in Exp. 68 and 72A of his series, has demonstrated that benzoate of soda is a powerful hepatic stimulant.

From the connection of benzoic acid and the benzoates with the production of hippuric acid, the influence of these drugs upon the urine has received a considerable amount of attention, though only two really careful scientific experiments have hitherto been made upon the action of the benzoates upon the nitrogen of the urine.

Klitzinsky (*Öst. Ztsch. f. pract. Heilk.*, Bd. iv. S. 41, 1858) comes to the conclusion that no alteration in the nitrogenous matter of the urine occurs. I have been unable to procure the original paper, which is referred to in Hermann's *Handbuch der Physiologie*, vol. vi. p. 172.

Meissner and Shepard, in their admirable paper "*Ueber das Entstehen der Hippursäure im thier. Organismus*," Hanover, 1866, show that when hippuric acid appears in the urine after the administration of benzoic acid, the urea is not diminished.

Salkowski (*Ztsch. f. Physiol. Chem.*, Bd. i. S. 45, 1877) has recorded two very careful experiments on the influence of benzoate of soda. The diet of the dog upon which these observations were conducted was carefully regulated, and a nitrogenous balance (*stickstoffgleichgewicht*) established.

The following results were obtained :—

Date.	W. of Dog in Kilos.	Urine to c.ca.	Sp. G.	N. Bunsen's Method.	H ₂ SO ₄ as BaSO ₄ .	Remarks.
16. 7.75	19.62	400	1014.5	3.377	0.868	
17			1014.5	3.480	0.880	
18	19.65		1018.5	3.208	0.842	
*19		400	1028.5	4.865	1.332	5.12 grms. benzoic acid as soda salt.
*20	19.62	400	1035.0	5.648	1.344	7.323 grms. benzoic acid as soda salt.
21	19.55	400	1014.5	3.976	0.783	
22	19.47	400	1014.5	3.132	0.864	
23	19.25	400	1015	3.440	0.840	
24	19.03	400	1015	3.568	0.850	
*25	19.06	425	1037	5.872	1.512	7.588 grms. benzoic acid as soda salt.
*26	19.00	400	1038	5.652	1.206	7.527 grms. benzoic acid as soda salt.
27	18.83	400	1015	4.024	0.524	
28	18.73	410	†	3.523		

Bunge and Schmiedeberg, in their paper on hippuric acid (*Arch. f. Exp. Pathol.*, Bd. vi.), do not consider the influence of benzoates upon the nitrogen excreted.

C. Virchow (*loc. cit.*) has made two experiments, under Salkowski's direction, and finds a well-marked rise in the daily excretion of nitrogen under the influence of benzoic acid given as the soda salt. His results agree so entirely with those of Salkowski that it is unnecessary to reproduce them here.

In regard to the action of benzoates upon the uric acid, it was long ago stated by Wöhler and Keller (*Ann. der Chem. u. Pharmac.*, xliii. S. 108) that no decrease in the uric acid occurred.

More recently, Garrod has investigated the subject, and has come to the conclusion that benzoates do very decidedly diminish the amount of uric acid excreted ("Lettsomian Lecture," *Brit. Med. Jour.*, 1883, vol. i.). His method of experiment was not altogether satisfactory. The urine of the 24 hours was not dealt with, and apparently no attempt was made to fix the diet. I here quote his last experiment (Exp. IV.), which gives results exactly similar to the other three, and will serve as an illustration of his method of procedure.

I. Urine from 11 A.M. to 2 P.M., after 60 grs. of benzoate of soda :

Urine = $5\frac{3}{4}$ oz.

Uric acid = 0.17 grs.

II. Urine from 11 A.M. to 2 P.M., after 120 grs. of benzoate of soda :

Urine = $9\frac{1}{2}$ oz.

Uric acid = 0.57 grs.

III. Urine as above. No benzoate for 27 hours :

Urine = 8 oz.

Uric acid = 1.00 grs.

IV. Urine as above. No benzoate for 51 hours :

Urine = 12 oz.
 Uric acid = 1.25 gra.

V. Urine as above. No benzoate for 75 hours :

Urine = 10 oz.
 Uric acid = 1.00 gra.

Cook (*Brit. Med. Jour.*, 1883, vol. ii. p. 9) opposes these conclusions, and contends that the diminution observed by Garrod was due to the presence of benzoic acid in the urine preventing the crystallisation of the uric acid.

Using the method of uric acid determination devised by himself, he gets the following results. The experiment was made upon a man with fixed diet:—

Date.	Uric Acid.	Remarks.
May 14	13.0 gra.	
15	12.3 "	
16	13.0 "	
17	...	
18	13.2 "	
19	13.0 "	
20	...	
21	12.4 "	30 gra. benzoate of soda.
22	13.7 "	60 " " "
23	14.0 "	40 " " "
24	13.2 "	60 " " "
25

The question of the influence of benzoates upon the uric acid must therefore be regarded as undecided, and as requiring further elucidation.

Exp. V.

The influence of benzoate of soda in the water, urea, and uric acid is shown in the accompanying table and abstract, and in fig. 4.

The production of hippuric acid has already been so fully studied, that it was considered unnecessary to make any estimation of the amount produced.

Its disturbing influence on the accuracy of the hypobromite method for the estimation of urea need not be considered, since Knop (*Ber. d. könig. Sächs. Gesell. d. Wissen.*, 1870, p. 17), and Hüfner (*J. f. pract. Chemie N. F.*, Bd. iii. 1871, p. 18), have shown that none of the nitrogen of hippuric acid is evolved.

The possible disturbing influence of hippuric and benzoic acid in the urine upon Haycraft's method for uric acid had, however, to be investigated.

Exp. VA.

Does the presence of benzoates in the urine influence the accuracy of Haycraft's method of uric acid estimation?

Using Haycraft's process, the urine of the 15th Feb. yielded 0.04% of uric acid.

To 25 c.cs. of this urine 0.2 grms. of benzoate of soda were added. The uric acid was again determined by the same method, and was found to amount to 0.039%.

Exp. VB.

Does the presence of hippuric acid vitiate the accuracy of Haycraft's method?

To 25 c.cs. of the same urine, 0.2 grms. of hippuric acid was added, and the uric acid, determined as before, was found to be 0.041%.

Therefore the presence of benzoates and of hippuric acid do not interfere with the accuracy of this process.

On the 16th the urine contained a faint trace of albumin, and reduced Fehling's solution very remarkably, giving on boiling a copious orange-coloured precipitate. So marked was this reduction, that I felt convinced that sugar was present and endeavoured to make a quantitative analysis. The amount of Fehling's solution reduced indicated the presence of 4% of sugar.

With Böttcher's test the bismuth was only slightly reduced, giving a greyish colour.

The fermentation test was also tried, and after several days gave no evolution of gas, although a check experiment with the same yeast yielded an abundance of carbonic acid.

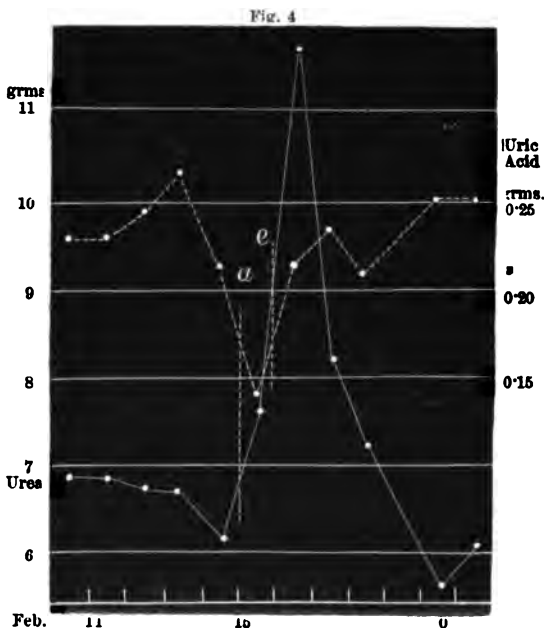
The reduction is due to the presence of a substance described by Salkowski in a short note in the *Zeitsch. f. Physiol. Chem.*, Bd. iv. S. 135. Its exact composition has not been determined.

The urine of the 17th gave a still more marked reduction of the cupric salt, but no evolution of carbonic acid occurred on the addition of yeast.

On the 18th the reduction was decidedly less.

Exp. V.

Date.	Urine in c.cs.	Sp. G.	Urea in grms.	Uric acid in grms.	Bowels.	Remarks.
11. 2. 85	745	1009	6.910	0.230	not moved	Weight of dog=13.6 kilos. Diet—Oatmeal 113 grms. Milk, 320 c.c.
12	745	1009	6.910	0.230	moved	
13	625	1011	6.700	0.247	not moved	
14	625	1010	6.700	0.268	moved	7.0 grms. benzoate of soda=0.51 gm. per kilo. 7.5 grms. benzoate of soda=0.55 gm. per kilo.
15	530	1013	6.065	0.212	not moved	
16	650	1017	7.540	0.130	moved	
17	800	1023	11.680	0.216	not moved	
18	710	1011	8.236	0.232	" "	
19	700	1010	7.140	0.210	" "	
20	Urine lost				" moved	
21	500	1012	5.800	0.253	not moved	
22	760	1010	6.080	0.253	" "	



Exp. V.—Excretion of Urea and Uric Acid (under) Benzoate of Soda. 7 grms. given at *a*, and 7.5 grms. at *e*.

Average Daily Excretion of various Constituents
under Benzoate of Soda.

	Before.	With.	After.	Before and After.	With.	Percentage Change.
Water, in c.ca.	654	720	653	653.5	720	+ 10.00%
Urea, in grms.	6.663	9.152	5.840	6.251	9.152	+ 46.4%
Uric Acid, , ,	0.236	0.195	0.236	0.236	0.195	- 17.8%

Exp. VI.

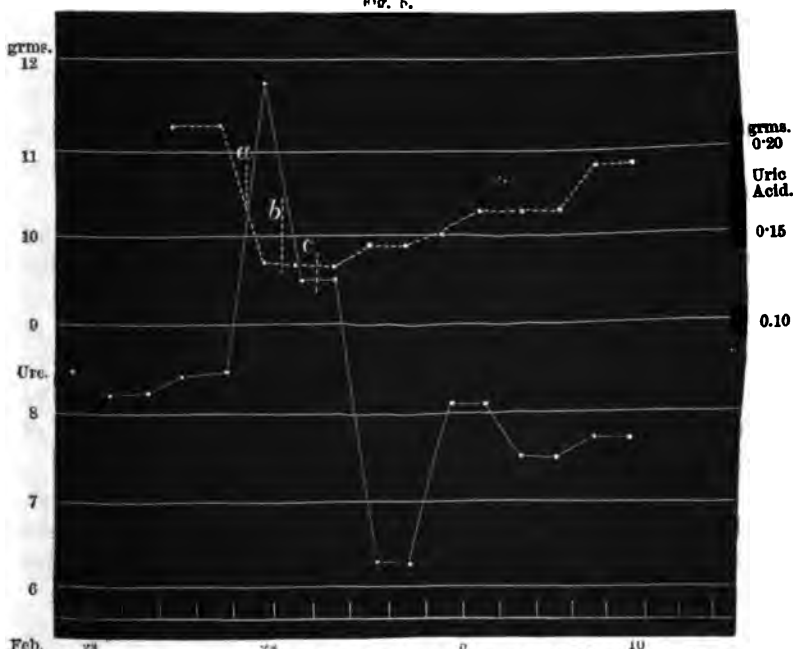
During the administration of the drug, which was given in the form of a pill made up with a little mucilage, the reducing power of the urine on Fehling's solution was well marked.

The influence of the drug is shown in the table and abstract, and in fig. 5.

Exp. VI.

Date.	Urine in c. ca.	Sp. G.	Urea in grms.	Uric Acid in grms.	Remarks.
23. 2. 85	900	1009	8.550		Weight of dog—13.154 kilos. Diet as in previous experiments.
24	800	1010	8.550		
25	800	1011	8.335		
26	675	1010	8.482	0.218	
27	675	1011	8.482	0.218	
28	650	1022	11.700	0.186	7 grms. benzoate of soda—0.53 gram. per kilo. 8 grms. benzoate of soda—0.6 gram. per kilo. 7.5 grms. benzoate of soda—0.57 gram. per kilo.
1. 3.	700	1015	6.160	0.182	
2	700	1024	13.020	0.182	
3	590	1010	6.308	0.142	
4	590	1013	6.308	0.142	
5	675	1012	8.140	0.152	
6	675	1012	8.140	0.164	
7	710	1010	7.550	0.164	
8	710	1011	7.550	0.164	
9	742	1010	7.717	0.190	
10	742	1011	7.717	0.190	

Fig. 5.



Feb. 23 28 3 10
Exp. VI.—Excretion of Urea and Uric Acid under Benzoate of Soda. 7 grms. given at a, 8 grms. at b, and 7.5 grms. at c.

**Average Daily Excretion of various Constituents under
Benzoate of Soda.**

	Before.	With.	After.	Before and After.	With.	Percentage Change.
Water, in c.cs. . .	793	683	664	728	683	- 6.3%
Urea, in grms. . .	8.425	10.293	7.596	8.010	10.293	+ 28.5%
Uric Acid, ,, . .	0.287	0.183	0.159	0.198	0.133	- 32.8%

Results.—My experiments merely confirm the observations of Salkowski and Virchow in regard to the uræa excreted.

They also show that in the dose given benzoate of soda has practically no influence upon the amount of water excreted.

The point of chief interest is the clear demonstration afforded that benzoate of soda really does diminish the uric acid excretion.

At present I cannot discuss the relationship of the hippuric acid produced to this diminution in the uric acid. It is a matter of great importance which I hope further to investigate.

III. COLCHICUM.

On the cholagogue action of colchicum Rutherford gives two experiments (Exp. 17 and 18), which show that this drug is undoubtedly an hepatic stimulant and a powerful hydrocathartic. The dose of the aqueous extract used in these experiments was large—60 grs. being given.¹

The influence of colchicum upon the urinary secretion, and upon the urinary constituents has, from the connection of this drug with the treatment of gout, been much studied clinically.

All the earlier observations on the subject, as those of Chelius (Lewins, *Ed. Med. and Surgical Jour.*, 1841, p. 200), of Christison and MacLagan (*Ed. Month. Jour. of Med. Sc.*, 3d series, vol. xvi. p. 24), are valueless, as the daily amount of urine is not taken into consideration.

Boecker (*Beiträge zur Heilkunde*, Crefeld, 1849) concludes that colchicum has practically no effect on the renal secretion, but his experiments show too many fallacies to allow of his conclusion being accepted.

Krahmer (*Jour. f. Pract. Chemie*, Bd. 41) gives the following

¹ In all probability the sample used was not freshly prepared.

table, showing the effect of the administration of colchicum on the various constituents of the urine in grms:—

	Amount.	Dry Residue.	Combustible Components.	Ash.	Urea.	Uric Acid.
Mean of 62 observations without the drug in usual condition,	2084·6	74·008	39·654	35·242	19·640	0·361
Mean of 5 observations during the use of tinct. colchici seminum in doses of 1 to 5 drachms,	1756·5	71·987	42·259	29·728	22·843	0·684

Hammond (*Proc. Philad. Acad. Nat. Sc.*, Dec. 1858, p. 18) gives a series of experiments upon the vegetable diuretics. He finds that, while digitalis, juniper, and squills increase the water excreted, colchicum alone increases the solid constituents. His experiments were conducted upon a healthy man, with slight precautions in regard to diet and exercise. The following table gives his results:—

	Urine.	Sp. G.	Total Solids.	Inorganic.	Organic.
Normal standard,	1280	1025	63·12	29·83	33·29
Under colchicum,	1556	1023	77·28	35·23	42·04

S. R. Percy's paper on the subject of the influence of colchicum upon the uric acid excretion (*Amer. Med. Times*, 1862) is absolutely valueless, as the method adopted for estimating the uric acid—by observing the amount of precipitate—is exceedingly crude and fallacious.

Garrod, in his admirable "Treatise on Gout and Rheumatic Gout," has given the results of a tolerably full investigation into the action of colchicum upon the uric acid, and of one or two observations on its influence upon the urea. Two experiments upon healthy patients are given.

In his first experiment the average amounts of water and of uric acid were as follows:—

For four days before administration of any drug—

Water averaged 68·5 fl. oz. per diem.

Uric acid ,, 8·24 gra. ,, ,,

For five days under colchicum the average was—

Water	55·6 fl. oz. per diem.
Uric acid	„ 7·67 grs. „ „

In his second experiment the averages for three days before the drug was given were—

Water	= 37·7 fl. oz.
Uric acid	= 5·03 grs.

Averages for five days while drug was given—

Water	= 25·2 fl. oz.
Uric acid	= 529 grs.

From a more careful study of the details of these experiments we see that nothing can be deduced from them. The daily variations in the uric acid excreted were very great, and completely vitiated the results.

Garrod also gives six observations on the urine of gouty patients. Observations on the action of a drug in disease are of little value, and we therefore refrain from quoting these experiments.

From his observations he is led to the following conclusions:—

“1. There is no evidence that colchicum produces any of its effects upon the system by causing the kidneys to eliminate an increased quantity of uric acid; in fact, when the drug is continued for any length of time it appears to exert a contrary effect.

“2. We cannot assert that colchicum has any effect upon the excretion of urea or the other solid ingredients of the urine.

“3. Colchicum does not act as a diuretic in all cases; on the contrary it often diminishes the quantity of urine, more especially when it produces a marked effect on the alimentary canal.”

Certainly, in respect to the action of colchicum upon the urea and uric acid, Garrod has little ground upon which to base his conclusions. Painstaking and careful as are his experiments they are open to all the many fallacies of clinical observation; while his use of the old method of Heintz for the estimation of uric acid renders even his analysis open to objection.

Obviously the question of the action of colchicum on the urea and uric acid of the urine must be regarded as totally unsettled and requiring careful experimental study.

Exp. VII.

In this experiment very large doses of the drug were given, and as is seen in the abstract a much smaller percentage increase of the urea occurred than in the next experiment. The marked purgation which was induced may have prevented a greater increase in the urea excretion.

The influence of colchicum on the uric acid is not well illustrated in this experiment—though on the second day of the administration of the drug a well-marked rise occurred. In all probability the diarrhoea induced had something to do with the great fall which occurred on the third day.

Exp. VII.

Date.	Urine in c.ca.	Sp. G.	Urea in grms.	Uric Acid in grms.	Bowels.	Remarks.
15.12.24	620	1010	6.262	0.1041	moved	Weight of dog=12.68 kilos. Diet as in previous experiment. 0.5 grm. acetic extract of colchicum=0.039 grm. per kilo. 1.0 grm. acetic extract of colchicum=0.078 grm. per kilo. 1.1 grm. acetic extract of colchicum=0.086 grm. per kilo.
16	460	1011	5.520	0.1381	not moved	
17	565	1012	6.780	0.1911	moved	
18	520	1013	7.900	0.1394		
19	540	1014	8.262	0.2106	copious soft semi-fluid evacuation	
20	425	1016	8.062	0.0858	copious soft evacuation	
21	492		7.718	0.0800	several watery evacuations	
22	492		7.718		not moved	
23	400	1013	6.560		moved	

Average daily Excretion of the various Constituents under the influence of Colchicum.

	Before Drug.	With Drug.	After Drug.	Before and After.	With.	Percentage Change in.
Water, in c.ca.	548	495	461	504	495	-1.6%
Urea, in grms.	6.187	8.041	7.332	6.759	8.041	+18.1%

The uric acid is not given in this table, as it was not estimated on the two days succeeding those on which colchicum was given.

Exp. VIII.

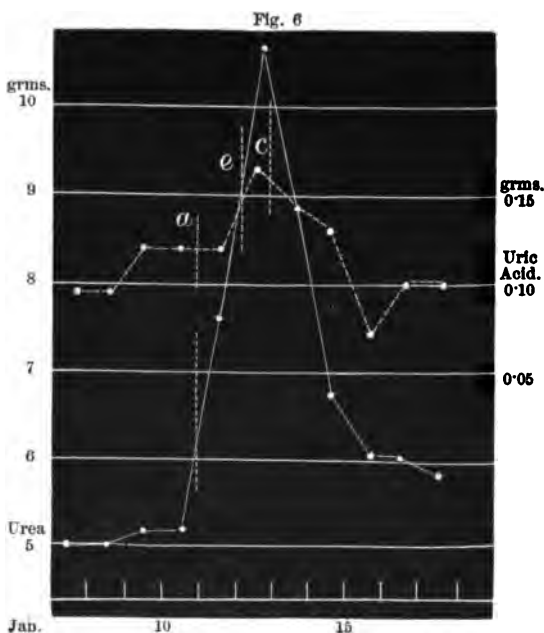
The influence of moderately large doses of the acetic extract of colchicum on the water, urea, and uric acid daily excreted is shown in the accompanying table and abstract, and in fig. 6.

In this experiment the chief point of interest, apart from the special
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action of colchicum, is the illustration it affords of the influence of purgation. On the 12th and 14th a copious soft motion followed the administration of the drug, and the urea was only slightly increased, while upon the 13th, when the bowels were not moved, a greater rise occurred.

Exp. VIII.

Date.	Urine in c.cs.	Sp. G.	Urea in grms.	Uric Acid in grms.	Bowels.	Remarks.
8.1.85	375	1013	5.045	0.095	moved	Weight of dog = 13.6 kilos. Diet as in previous experiment.
9	375	1013	5.045	0.095	"	
10	470	1012	5.140	0.124	not moved	
11	470	1011	5.140	0.124	"	
12	520	1014	7.644	0.122	copious soft motion	0.5 grm. acetic ext. colchid = 0.087 per kilo.
13	630	1015	10.726	0.167	not moved	0.3 grm. acetic ext. colchid = 0.02 per kilo.
14	610	1016	8.834	0.142	copious soft motion	0.4 grm. acetic ext. colchid = 0.029 per kilo.
15	475	1014	8.692	0.132	moved	
16	498	1013	8.040	0.070	not moved	
17	498	1012	8.040	0.107	moved	
18	550	1011	5.940	0.107	not moved	



Exp. VIII.—Excretion of Urea and Uric Acid under Colchicum. 0.5 grm. of acetic extract given at *a*, 0.3 grm. at *e*, and 0.4 grm. at *c*.

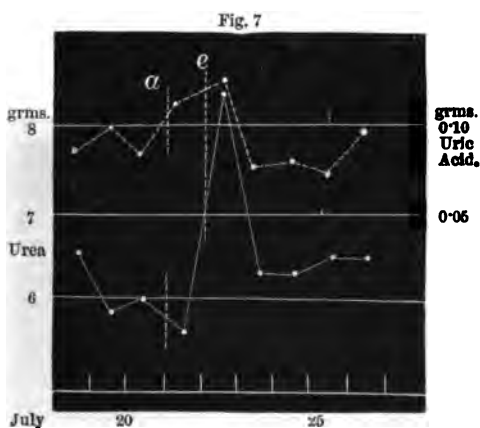
Average daily Excretion of various Constituents under Colchicum.

	Before Drug.	With Drug.	After Drug.	Before and After.	With.	Percentage Change in.
Water, in c.ca.	422	588	505	463	588	+25.9%
Urea, in grms.	5.092	9.068	6.178	5.685	9.068	+60.9%
Uric Acid, ..	0.109	0.148	0.102	0.105	0.148	+36.1%

Exp. IX.

In this experiment a recently prepared sample of acetic extract of colchicum was used. This probably accounts for the great purgation induced by small doses.

Date.	Urine in c.ca.	Sp. G.	Urea in grms.	Uric Acid in grms.	Bowels.	Remarks.
19.7.85	640	1009	6.528	0.088	moved	Weight of dog=13.37 kilos.
20	580	1009	5.916	0.097	"	Diet as in former experiments.
21	640	1009	6.016	0.088	not moved	
22	700	1008	5.800	0.119	moved—copious soft	0.2 grm. acet. ext. colchici (fresh) =0.014 grms. per kilo.
23	740	1010	8.314	0.126	moved—soft, mucous evacuation	0.2 grm. acet. ext. colchici (fresh) =0.014 grms. per kilo.
24	645	1008	6.242	0.074	moved—loose	
25	645	1009	6.242	0.077	moved	
26	480	1010	6.480	0.070	"	
27	480	1010	6.480	0.066	"	



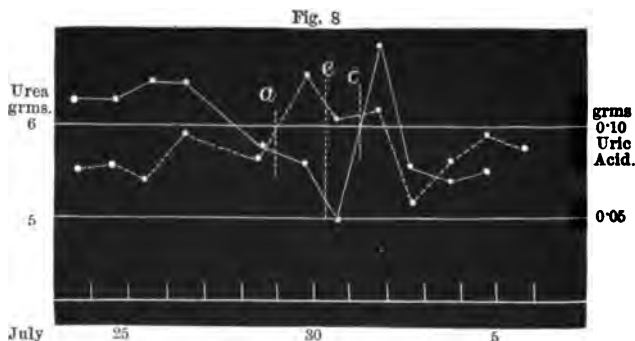
Exp. IX.—Excretion of Urea and Uric Acid under Colchicum. 0.2 grm. acetic extract given at *a*, again at *e*. Very free purgation induced.

Average daily Excretion of various Constituents under Colchicum.

	Before Drug.	With Drug.	After Drug.	Before and After.	With.	Percentage Change in.
Water, in c.cs.	620	720	562	591	720	+21·8%
Urea, in grms.	6·225	6·957	6·417	6·321	6·957	+10%
Uric Acid, „	0·087	0·122	0·079	0·083	0·122	+47%

Exp. X.

Date.	Urine in c.cs.	Sp. G.	Urea in grms.	Uric Acid in grms.	Bowels.	Remarks.
24.7.85	{ 645	1008	6·842	0·074	moved	Weight of dog=13·15 kilos.
25	{ 645	1009	6·842	0·077	„	Diet as in previous experiments.
26	{ 480	1010	6·490	0·070	„	
27	{ 480	1010	6·490	0·066	„	
28	„	
29	520	1010	5·772	0·087	„	
30	580	1009	5·563	0·128	not moved	0·15 grm. acet. ext. colchici=0·0114 gram. per kilo.
31	620	1009	4·960	0·104	moved—very loose	0·20 grm. acet. ext. colchici=0·0147 gram. per kilo.
1	605	1011	6·836	0·109	moved—very loose	0·20 grm. acet. ext. colchici=0·0147 gram. per kilo.
2	{ 530	1013	5·500	0·057	moved	
3	{ 530	1007	5·500	0·075	„	
4	620	1009	5·300	0·091	„	
5	620	1009	5·456	0·085	„	



Exp. X.—Excretion of Urea and Uric Acid under Colchicum.
0·15 grm. of acetic extract given at a, 0·2 grm. at e, and again
at c.

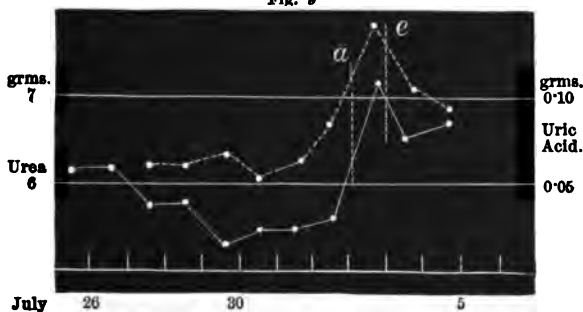
Average Daily Excretion of the various Constituents under Colchicum.

	Before Drug.	With Drug.	After Drug.	Before and After.	With.
Water, in c.cs. . .	548	571	606	557	571
Urea, in grms. . .	6.204	5.786	5.453	5.828	5.786
Uric Acid, ,, . .	0.081	0.113	0.077	0.079	0.113
Percentage change in					
Water,					practically unaltered
Urea,					"
Uric acid,					+ 43%

Exp. XI.

Date.	Urine in c.cs.	Sp. G.	Urea in grms.	Uric Acid in grms.	Bowels.	Remarks.
26.7.85	550	1009	6.182	...	moved	Weight of dog=13.25 kilos. Diet as in previous experiments.
27	550	1009	6.182	...	"	
28	620	1009	5.816	0.0621	"	
29	620	1008	5.816	0.0621	"	
30	620	1010	5.332	0.0682	"	
31	562	1010	5.454	0.0626	"	0.2 grm. acet. ext. colchici=0.015 gram. per kilo. 0.2 grm. acet. ext. colchici=0.015 gram. per kilo.
1.8	562	1010	5.454	0.0606	"	
2	620	1009	5.564	0.0806	"	
3	780	1009	7.176	0.141	moved—rather loose	
4	720	1009	6.523	0.106	moved—very loose	
5	700	1009	6.720	0.091	not moved	

Fig. 9



Exp. XI.—Excretion of Urea and Uric Acid under Colchicum. 0.2 grm. of acetic extract given at a, and again at e.

**Average Daily Excretion of various Constituents under
Colchicum.**

	Before. Drug.	With. Drug.	Percentage Change in.
Water, in c. ca.	577	785	+27·3
Urea, in grms.	5·743	6·784	+18
Uric Acid,	0·0646	0·112	+73·3

Results.—The above five experiments clearly show that in medium doses colchicum increases the water and urea excretion to a moderate amount, and the uric acid excretion to a much greater extent. Indeed the most striking feature of these experiments is the very marked increase in the uric acid production indicated by them, an increase which renders it difficult to explain the well-known beneficial action of this drug in gout. For, that an increased production and not merely an augmented excretion is indicated by these experiments is proved by the fact that after the administration of the drug is discontinued no great fall below the normal daily excretion occurs.

IV. PERCHLORIDE OF MERCURY.

Experiments 78A, 78B, 78C, and 78D of Professor Rutherford's series clearly show that perchloride of mercury is a cholagogue of considerable power.

In spite of the length of time during which mercury has, in different forms, been largely employed in medicine, I can only find one or two experiments on its action on the tissue metabolism (*stoffwechsel*), as estimated by the amount of nitrogen excreted.

Harvey (*Brit. and For. Medico-Chir. Rev.*, vol. xxix. p. 515) records a series of experiments on the action of blue pill mass and perchloride of mercury upon the urea excretion in dogs.

The dogs were kept in a cage, the urine being collected much as in my own experiments. The diet consisted of "paunch." This is a form of dog's meat sold in London, and consists, I believe, in the intestine, stomach, liver, &c., of sheep and oxen.

In Exp. I. the dog got 6 oz. of "paunch" and $\frac{1}{2}$ pint of water

daily. For seven days before the administration of the drug the urine was daily collected and the urea estimated.-

During the next fourteen days the pil. hydrarg. was given in doses, commencing at $2\frac{1}{2}$ gra. and increased to 15 grs., so that in the fourteen days 100 grs. of the drug were taken. The following table gives the average excretion of water and urea before and under the administration of the drug.

	Before	With
Water .	203·187 grms.	212·39 grms.
Sp. G. .	1041	1043
Urea .	13 grms.	12·9 grms.

In Exp. II. the dog got 12 oz. of "paunch" and $\frac{1}{2}$ pint of milk. For nine days no drug was given, then for nine days the liquor hydrargyri perchloridi of the pharmacopœia in doses of one or two drachms. The larger dose produced diarrhœa.

Average daily excretion before and with the drug :—

	Before	With
Water .	393·687 grms.	315·7 grms.
Sp. G. .	1026	1031
Urea .	8·515 grms.	8·580 grms.

During this experiment the water and urea excreted varied much from day to day.

Exp. III. was similar to Exp. II., but the dog was kept for twelve days without the drug, and for twenty-one days it had daily the liquor hydrargyri perchloridi in doses of from one to two drachms. The following results were obtained :—

Average daily excretion before and with the drug :—

	Before.	With.
Water .	339·06 grms.	342·77 grms.
Sp. G. .	1030	1024
Urea .	15·9 grms.	14·323 grms.

During these experiments the dogs are said to have enjoyed perfect health.

Unfortunately these experiments are not satisfactory. The diet given was much too liberal, and we find in consequence very large daily variations in the amounts of water and of urea excreted. Besides such a substance as "paunch" is not of sufficiently fixed a composition to render it suitable for such experiments.

The only other observation of any value which I have been able

to find is by Hermann v. Boeck (*Zeitsch. f. Biol.*, vol. v. p. 393). It is to be regretted that this most careful observation was not made upon a healthy man. Unfortunately a syphilitic case was selected, so that the results obtained must be accepted with great caution.

The method of experiment was ingenious and admirable. The nitrogen contained in the diet was estimated and compared before and under the administration of the drug with the nitrogen excreted by the kidneys and in the fæces.

The diet was liberal, consisting of eggs, bread, milk, beef extract or soup, beer, butter, and salt.

The patient was a man aged 44, who had been infected with syphilis three months before, and who suffered at the time from secondary syphilis, condylomata, &c. On the 10th of Oct. he was put upon a fixed diet, and from the 12th to the 15th the urea excretion was nearly constant. On the 15th mercurial inunctions were commenced. On the 20th salivation occurred, and on the 22nd the eighth and last inunction was given.

Boeck gives a full table of the nitrogen in the diet, the amount of urine, the sp. gr., the urea, the nitrogen in the urine, and the nitrogen in the fæces.

The following table shows his results, so far as they concern the present question:—

Date.	Remarks.	Nit. of Diet.	N. Excreted.	Urea.
10		16.1	12.4	26.7
11		16.7	17.4	30.7
12		17.1	16.3	31.3
13		17.7	18.6	34.5
14		17.3	17.5	32.0
15	Inunction daily till 22nd.	17.3	18.6	34.9
16		17.5	18.8	35.0
17		17.5	18.9	33.9
18	<i>Some Diarrhæa.</i>	17.8	19.2	33.1
19		17.5	18.5	35.4
20		17.4	19.2	37.0
21		17.8	18.0	35.5
22	<i>Diarrhæa.</i>	17.5	19.0	33.1
23		17.5	18.0	32.3
24		17.7	17.9	33.3
25		17.7	17.9	32.8

Before the inunctions—from the 12th to the 15th

52.1 grms. of nitrogen were taken in }
52.4 " " " excreted } = + 0.5%

During the application period—

193.2 grms. of nitrogen taken in }
204.0 grms. of nitrogen excreted } = + 5.6%

I cannot agree with Boeck's conclusion that, "Dieses Plus ist ganz unwesentlich und beruht zum Theil auf Fehlern der Methode, zum Theil vielleicht auf den Diarrhoën, die mehr stickstoffhaltige stoffe den Körper entführten."

Exp. XI.

The perchloride of mercury was given in pills made up with starch. Even with the dose given, 0.037 grms., which was large, absolutely no physiological effects were produced, and it is extremely probable that the drug was never absorbed, but that the pills passed through undigested.

Exp. XII.

The results of Experiment XI. were negative, probably, as before stated, on account of the form in which the drug was given.

Experiment XII. was made on another dog weighing 13.14 kilos, which had been kept for more than a month upon a diet similar to that used in the former experiments. Before the drug was given it had been for more than a week excreting an almost equal amount of urea each day. The drug was given in the form of a pill, made up with a very small quantity of oatmeal and gum. During and following the administration of the drug no constitutional symptom could be detected.

Exp. XII.

Date.	Urine in c.ca.	Sp. G.	Urea in grms.	Uric Acid in grms.	Bowels.	Remarks.
18. 4. 85	580	1010	6.148	0.075	moved	Weight of dog=13.14 kilos. Diet as in previous experiments.
19	650	1010	6.500	0.084	"	
20	685	1010	6.500	...	"	
21	685	1011	6.500	0.102	"	
22	685	1009	6.773	0.084	"	
23	685	1010	6.773	0.108	"	0.02 grm. perchloride of mercury in pill=0.0015 grm. per kilo.
24	605	1011	6.715	0.138	"	
25	740	1010	7.400	0.148	"	
26	780	1009	6.552	0.101	"	0.04 grm. perchloride of mercury in pill=0.0080 grm. per kilo. 0.05 grm. perchloride of mercury in pill=0.0088 grm. per kilo.
27	655	1011	7.598	0.085	"	
28	810	1015	14.580	0.187	"	
29	745	1009	7.008	0.097	"	
30	680	1011	6.300	0.082	"	

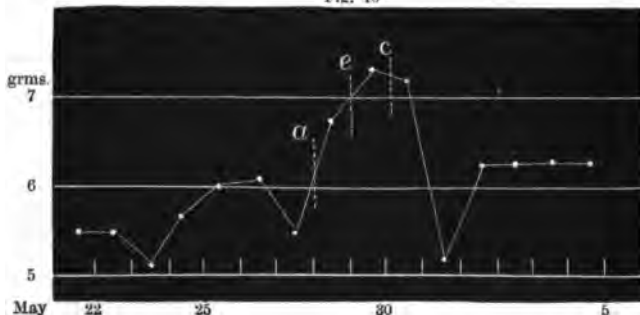
Average Daily Excretion of the various Constituents under
Perchloride of Mercury.

	Before Drug.	With Drug.	After Drug.	Before and After.	With.	Percentage Change in.
Water, in c.c.s. .	689	745	680	684	745	+17%
Urea, in grms. .	6.584	7.978	6.800	6.408	7.978	+24%
Uric Acid, ,, .	0.098	0.107	0.082	0.090	0.107	+18.8%

Exp. XIII.

Date.	Urine in c.c.s.	Sp. G.	Urea in grms.	Uric Acid in grms.	Bowels.	Remarks.
22.5.85	517	1010	5.457	0.078	moved	Weight of dog=18.27 kilos. Diet, as in previous experiment.
23	517	1010	5.457	0.078	"	
24	560	1010	5.170	0.088	"	
25	560	1010	5.600	0.089	"	
26	700	1008	6.020	0.091	"	
27	680	1008	6.072	0.116	"	
28	620	1008	5.454	...	"	
29	706	1007	6.768	0.118	"	0.0166 grm. HgCl ₂ in iodide of potassium solution=0.0012 grm. per kilo.
30	600	1010	7.330	0.088	"	0.083 grm. HgCl ₂ in iodide of potassium solution=0.0023 grm. per kilo.
31	670	1010	7.236	0.088	"	0.066 grm. HgCl ₂ in iodide of potassium solution=0.0049 grm. per kilo.
1-6	600	1010	5.180	0.078	"	
2	622	1008	6.310	0.078	"	
3	622	1008	6.310	0.094	"	
4	606	1008	6.310	0.092	"	
5	606	1008	6.310	0.092	"	

Fig. 10



Exp. XII.—Excretion of Urea under Perchloride of Mercury in Potassic Iodide. 0.0166 grm perchloride given at a, 0.083 grm. at e, and 0.066 grm. at c.

RELATIONSHIP OF UREA FORMATION TO BILE SECRETION. 299

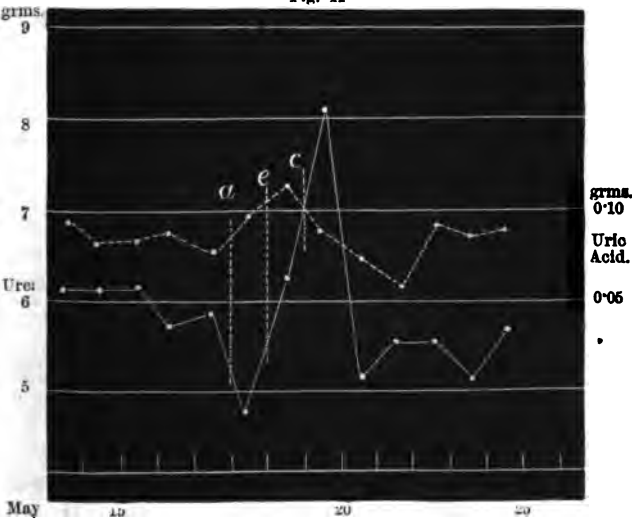
Average Daily Excretion of the various Constituents under Perchloride of Mercury.

	Before Drug.	With Drug.	After Drug.	Before and After.	With.	Percentage Change in.
Water, in c.cs. .	608	649	609	606	649	+ 7.09%
Urea, in grms. .	5.604	7.108	5.785	5.699	6.694	+ 21.5%
Uric Acid, ,, .	0.091	0.098	0.084	0.087	0.098	+ 12.6%

Exp. XIV.

Date.	Urine inc.cs.	Sp. G.	Urea in grms.	Uric Acid in grms.	Bowels.	Remarks.
13.5.86	570	1011	6.099	0.0957	moved	Weight of dog=18.87 kilos.
14	680	1010	6.114	0.0819	"	Diet of Oatmeal, 118.6 grms.
15	646	1010	6.144	0.0832	"	Milk, 820 c.cs.
16	510	1010	5.814	0.0856	"	
17	560	1010	5.985	0.0784	"	
18	590	1009	4.720	0.099	moved (soft)	0.05 grm. HgCl ₂ in pills of 0.025 grm. each=0.0087 grm. per kilo.
19	560	1011	6.216	0.112	moved	0.10 grm. HgCl ₂ in pills of 0.080 grm. each=0.0074 grm. per kilo.
20	675	1011	8.100	0.087	"	0.10 grm. HgCl ₂ in pills of 0.080 grm. each=0.0074 grm. per kilo.
21	420	1010	5.156	0.0705	"	
22	517	1009	5.457	0.063	"	
23	517	1010	5.457	0.094	"	
24	550	1010	5.170	0.088	"	
25	560	1010	5.600	0.089	"	

Fig. 11



Exp. XIV.—Excretion of Urea and Uric Acid under Perchloride of Mercury. 0.05 grm. given at c, 0.10 grm. at c, and 0.10 grm. at c.

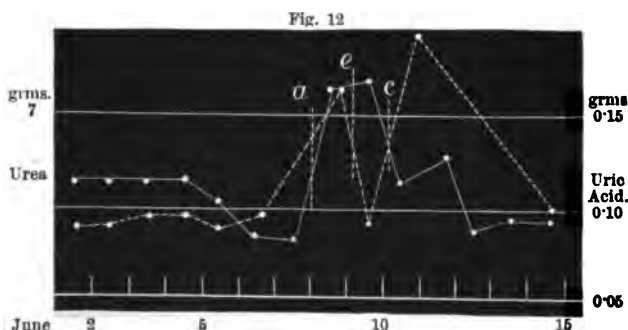
Average Daily Excretion of the various Constituents under
Perchloride of Mercury.

	Before Drug.	With Drug.	After Drug.	Before and After.	With.	Percentage Change in.
Water, in c.ca. .	582	608	513	547	608	+11.15%
Urea, in grms. .	6.021	6.345	5.346	5.683	6.345	+11.6%
Uric Acid, ,, .	0.085	0.099	0.079	0.082	0.099	+11%

Exp. XV.

Date.	Urine in c.ca.	Sp. G.	Urea in grms.	Uric Acid in grms.	Bowels.	Remarks.
2.6.85	{622	1008	6.310	0.088	moved	Weight of dog=13.37 kilos. Diet of Oatmeal, 113.4 grms. Milk, 320 c.c.
3	{622	1009	6.310	0.088	"	
4	{606	1008	6.310	0.092	"	
5	{606	1009	6.310	0.092	"	
5	{640	1008	6.016	0.088	"	
7	{652	1008	5.660	0.090	"	
8	{652	1009	5.660	...	"	
9	{670	1010	7.303	0.170	"	
						0.06 grm. HgCl ₂ in 0.5 c.c. satur- ated solution of potass. iodidi in gelatine capsule 0.0044 grm. per kilo.
10	606	1013	7.381	0.085	moved—loose	0.087 grm. HgCl ₂ in 0.5 c.c. saturated solution of potass. iodidi in gelatine capsule 0.0066 gram. per kilo.
11	710	1007	6.319	0.206	"	0.075 grm. HgCl ₂ in 0.5 c.c. satur- ated solution of potass. iodidi in gelatine capsule 0.0066 grm. per kilo.
12	560	1010	6.720	...	moved	
13	575	1007	5.750	...	"	
14	{562	1007	5.847	...	"	
15	{562	1007	5.847	0.096	"	

¹ Urine contains a distinct trace of albumen, and the fermentation test shows the presence of a small quantity of sugar.



Exp. XV.—Excretion of Urea and Uric Acid under Perchloride of Mercury in Solution of Potassic Iodide. 0.06 grm. given at *a*, 0.087 grm. at *e*, and 0.075 grm. at *c*.

Average Daily Excretion of various Constituents under
Perchloride of Mercury.

	Before Drug.	With Drug.	After Drug.	Before and After.	With.	Percentage Change in
Water, in c. cs. .	619	636	568	593	636	+7.2%
Urea, in grms. .	5.995	6.980	5.798	5.896	6.980	+17.5%
Uric Acid, ,, .	0.088	0.153	0.095	0.091	0.153	+68%

Results.—Both the perchloride of mercury and the iodide cause a distinct rise in the water, urea, and uric acid excretion. My reason for using the iodide will be explained in a future paper, while considering the nature of the relationship between the urea and bile-forming functions.

V. EUONYMIN.

Experiments 27 and 28 of Professor Rutherford's series show that euonymin is a powerful hepatic stimulant.

In regard to its action on the composition of the urine I can find only one observation, by Cook (*Brit. Med. Journal*, vol. i. 1883, p. 1060).

To a man kept on fixed diet, one grain of the drug was administered on an empty stomach on the days marked with an asterisk.

Date.	Urine.	Sp. G.	Urea.	Uric Acid.
Nov. 1*	38 oz.	1020	360 grs.	11.7 grs.
2*	34 "	1022	382 "	14.3 "
3*	50 "	1020	340 "	17.4 "
4	46 "	1020	375 "	14.3 "
5	43 "	1020	340 "	12.5 "

He concludes from this very insufficient experiment that while euonymin exerts no influence upon the urea excretion it increases the excretion of uric acid.

Practically nothing is known of the action of the drug upon the urinary constituents.

Exp. XVI.

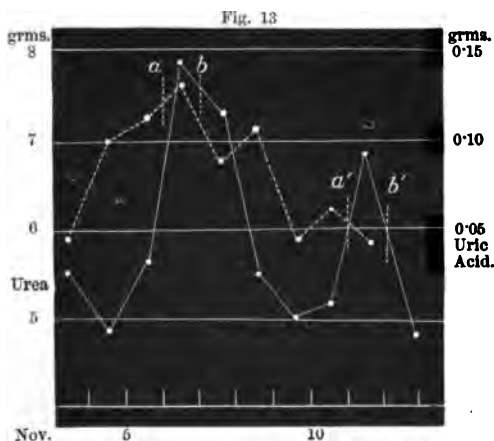
The dog had been upon a fixed diet from October 8, and had lost 3.17 kilos weight. It was, however, healthy and strong.

Before November 3 the variations in the daily urea excretion were considerable, but the average from October 28 to November 3 was 5.4 grms. per diem. From November 3 the daily excretion became more constant, and on the 7th 0.5 grms. of green euonymin, procured through Duncan & Flockhart from Kieth & Co., was administered in the form of a pill made up with a drop or two of alcohol, and next day 0.75 grms. were given.

The accompanying table, abstract, and fig. 13 show the influence of the drug upon the urine.

Exp. XVI. and XVII.

Date.	Urine in c.c.s.	Sp. G.	Urea in grms.	Uric Acid in grms.	Bowels.	Remarks.
4.11.24	450	1011	5.535	0.042	not moved	Weight of dog=12.23 kilos.
5	550	1011	4.840	0.100	"	Diet, Oatmeal=85 grms.
6	550	1011	5.650	0.110	moved	Milk, 300 c.c.
7	575	1013	7.977	0.182	"	Euonymin 0.5 grm.=0.041 grm. per kilo.
8	500	1015	7.358	0.083	"	Euonymin 0.75 grm.=0.06 grm. per kilo.
9	465	1014	5.580	0.109	not moved	
10	470	1013	5.000	0.047	moved	
11	450	1013	5.285	0.080	"	
13	455	1015	6.998	0.042	copious soft evacuation	Euonymin 1.5 grm.=0.1 grm. per kilo.
13	500	1010	4.800	...	copious soft evacuation	Euonymin 2.0 grm.=0.16 grm. per kilo.



Exps. XVI. and XVII.—Excretion of Urea and Uric Acid under Euonymin. 0.5 grm. given at *a*; 0.75 grm. at *b*; 1.5 grm. at *a'* and 2.0 grms. at *b'*.

Average Daily Excretion of the various Constituents under Euonymin.

	Before Drug.	With Drug.	After Drug.	Before and After.	With.	Percentage Change in
Water, in c.c.s.	56	537	461	488	537	+10.0%
Urea, in grms.	5.841	7.667	5.432	5.386	7.667	+42.3%
Uric Acid, ,,	0.084	0.107	0.072	0.078	0.107	+37.14%

Exp. XVII.

This is simply a continuation of Experiment XVI, larger doses of the drug being given, 1.5 grms. on the 12th, and 2.0 grms. on the 13th. On the second day the purgative action of the drug was very marked, while even on the 12th the motions were soft and unusually copious. It will be seen that, in this experiment, the urea was not so markedly increased as in the previous one, in fact that on the 13th, when the purgative action of euonymin was so manifest, a fall below the mean took place.

At the end of this experiment the dog was thin and looked ill. The diet was consequently increased and the uniform excretion of urea per diem was disturbed.

Exp. XVIII.

The dog had been upon the usual diet since November 14, and in spite of considerable daily variations, the average excretion of urea, from November 25 to December 1, was 7.02 grms. per diem.

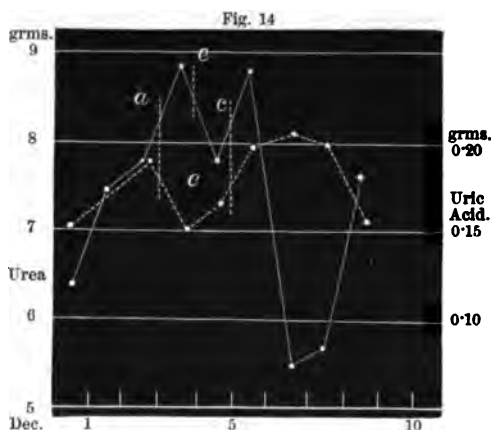
The experiment was commenced on December 1. Unfortunately the urines of the 2nd and 3rd were lost. On December 6, 1 gm. of green euonymin, made into a pill with absolute alcohol, was administered. Next day a similar dose was given; and on the 8th 1.5 gm. in the same form.

It is of interest to observe that upon the 7th, when a loose copious motion was produced by the drug, the urea was not nearly so manifestly increased as on the two other days.

The uric acid participated in the irregularity of the urea in its rate of elimination, and it appeared in this case to be uninfluenced by the drug, unless indeed the rise on the 8th, 9th, and 10th are to be considered as due to the euonymin.

Exp. XVIII.

Date.	Urine in c.c.s.	Sp. G.	Urea in grms.	Uric Acid in grms.	Bowels.	Remarks.
1.12.84	650	1008	6.240	0.154	moved	Weight of dog=12.16 kilos.
4	720	1012	7.421	..	not moved	Diet, Oatmeal, 112 grms.
5	690	1010	7.820	0.190	moved	Milk, 320 c.c.s.
6	750	1012	8.900	0.150	not moved	1.0 gm. Euonymin=0.08 gm. per kilo.
7	750	1010	7.725	0.165	soft motion	1.0 " =0.08 "
8	750	1012	8.795	0.202	moved	1.5 " =0.10 "
9	660	1009	5.499	0.204	"	
10	575	1010	5.582	0.201	"	
11	505	1014	7.777	0.156	"	



Exp. XVIII.—Excretion of Urea and Uric Acid under Euonymin. 1.0 grm. given at *a*, and at *c*, and 1.5 grm. at *c*.

Average Daily Excretion of the various Constituents under Euonymin.

	Before.	With.	After.	Before and After.	With.	Percentage Change in
Water, in c.ca.	683	750	578	628	750	+ 19%
Urea, in grms.	7.160	8.440	6.286	6.723	8.440	+ 20.3%

The uric acid is not given in this table, as a marked increase took place in the three days immediately following the administration of the drug.

Results.—1st. The water is slightly though distinctly increased under the action of euonymin. This is just what one would expect from the digitalis-like action of the drug.

2nd. The urea is very markedly increased, especially when purgation is not induced. Experiments 18 and 19 show well the influence of purgation in preventing the full action of the drug upon the urea and uric acid.

3rd. An increase in the uric acid is also indicated in Experiment XVII. concomitantly with, and in Experiment XIX. following, the administration of the drug.

Summary of Results.

1. *Salicylate of Soda.*—(A) *In man.* In dose of 0.106 grms. per kilo, salicylate of soda causes no change in the amount of water passed, a slight increase in the urea and a very marked

diminution in the uric acid excreted. This last change is by far the most manifest; in one experiment the diminution was as great as 64 per cent.

(B) *In dogs.* In doses of from 0.45 gm. to 0.6 gm. per kilo, salicylate of soda caused a marked diminution in the water passed, a rise in the urea, and a very great diminution in the uric acid excreted.

2. *Benzoate of Soda*, in doses of from 0.51 to 0.58 gm. per kilo, causes little or no change in the amount of water. The urea is greatly increased and the uric acid is diminished, though not so markedly as with salicylate of soda.

3. *Colchicum*, in doses of 0.02 to 0.037 gm. per kilo of the acetic extract (B.P.) causes a very marked increase in the urea and uric acid. When the doses are small the water is also increased, but with large doses the water secreted may actually fall, while neither the urea nor the uric acid are so markedly increased as with smaller doses.

4. *Perchloride of Mercury*, in doses of from 0.0015 to 0.0075 gm. per kilo, causes an increase in the excretion of water, urea, and uric acid.

5. *Euonymin*, in doses of from 0.04 to 0.10 gm. per kilo, causes a slight increase in the water excreted, and a very marked increase in the urea and uric acid. In larger doses, 0.16 grms. per kilo, it causes purging, with no diminution in the water passed by the kidneys, but without the marked rise in the urea excreted.

We thus see that in dogs, in a condition of nitrogenous balance, stimulation of the flow of bile by means of these drugs is accompanied by an increased urea production.

That an increased production and not merely an increased excretion of urea occurred is clearly shown by the fact that, after the administration of the drug was stopped, the amount of urea merely returned to the normal and did not manifest a fall corresponding to the initial rise.

I would therefore conclude that the formation of urea in the liver bears a very direct relationship to the secretion of bile by that organ. On the nature of this relationship I have not touched in the present paper, but at an early date I hope

to give the results of a series of experiments upon this subject.

To the physician the results of these observations must have considerable interest, especially of those which, dealing with the influence of salicylates and benzoates upon the uric acid excretion, afford a key to their mode of action in gout. No less interesting is the demonstration of the fact that colchicum increases and does not diminish the production of uric acid.

In conclusion, I have to tender my thanks to Professor Rutherford, who, by suggesting to me as a subject for research the influence of the action of the hepatic stimulants on the composition of the urine, induced me to undertake the present series of experiments. I have also to thank him for encouragement and advice during the prosecution of the work in the Physiological Laboratory of the University of Edinburgh.

RECENT HISTOLOGICAL METHODS. By WILLIAM HUNTER, M.B. (Edin.), M.R.C.S., *Late Assistant to the Professor of Physiology, Edinburgh University; former President of the Royal Medical Society, Edinburgh.*

WHILE engaged recently in working in the Pathological Institute in Leipsic, several methods employed in histology for hardening, embedding, cutting, and staining tissues, there in use, commended themselves so strongly for adoption, on account of their simplicity and effectiveness, that a short consideration of them at the present time may not be altogether without interest, perhaps value, to the many workers engaged in the same field of labour at home.

Owing to the cheapness of alcohol in Germany, most of the *hardening* of tissues is done by means of this agent; a method, however, even if it were always the better one, which can only have a very limited application with us; but under this heading, I would desire, in passing, to refer to a rapid method of hardening in Müller's fluid, first recommended by Weigert, which, so far as my experience goes, is worthy of a more extended trial. Weigert showed that, if the Müller's fluid be kept at a temperature of about 30° to 40° C., the hardening process is considerably accelerated, the tissues being ready for use in the course of ten days or a fortnight, instead of six weeks. This method is specially applicable to nervous tissues, *e.g.*, brain or spinal cord, and, from what I have seen of it, I can strongly recommend it as both speedy and effective. The jar containing the tissues is placed in a brood-oven (hatching-oven), maintained at the above temperature for the above length of time, the fluid being changed on the second, fourth, and seventh days, if necessary also on the tenth day. Another method of hardening, I would merely note in passing, is one which is made great use of by Gaule, of the Physiological Institute, Leipsic, *viz.*, placing the fresh tissue for twenty minutes or half an hour in a saturated solution of corrosive sublimate, and then hardening as usual in alcohol. The living tissues are in this way, as it were, fixed, and the method is specially suitable in carrying out minute histological observations.

The chief purpose of this paper, however, is to direct attention to the method of *embedding in celloidin*. Since its introduction, some two years ago now, into use in histology as an embedding agent, this substance has come to be very extensively employed, recommending itself, as it does, not only on account of its firmness, pliability, and its transparency when in thin sections, but also its cleanliness and the comparative ease with which it can be manipulated. It is obtainable either in the form of cakes, or as a fluid dissolved in ether. It is readily soluble in ether, slightly also in absolute alcohol. Although in mass it presents an opalescent appearance, in thin sections, clarified in the ordinary way by origanum oil or xylol, it is quite transparent, sometimes scarcely visible; and, at the same time that it firmly supports the tissue which is embedded in it, its presence in no way interferes with any of the necessary manipulations of the tissue, *e.g.*, staining, &c. It thus combines in itself several very striking advantages.

The method of embedding tissues in celloidin is the following:—The tissue, after having been hardened in alcohol, or, at least, immersed a sufficient length of time in alcohol to free it from water, is placed for twenty-four hours in a mixture of equal parts of alcohol and ether. If the tissue be of any size, it must be left in this mixture for twenty-four hours longer. It is then transferred into a thin solution of celloidin, made by dissolving a small piece of celloidin in an excess of ether, or better still in a mixture of equal parts of alcohol and ether, in which it is allowed to lie for twenty-four hours, after which it is thrown into a thicker solution of celloidin. In the latter it may be left for twenty-four hours, or even longer if necessary, the time varying with the size and thickness of the tissue. As a general rule, three days suffice to complete the process; twenty-four hours in alcohol and ether, twenty-four hours in thin celloidin, and twenty-four hours in the thicker celloidin. At the end of this time, the tissue has become thoroughly permeated with the celloidin, and our subsequent proceedings are directed towards enclosing it in a small solid block of this substance. This naturally can be effected by simply withdrawing the stopper from the bottle, and allowing the ether to evaporate till the whole of the celloidin solution has become solid, and we can

then cut our tissue out of this mass in a small square block. But a more convenient way, and one which involves less waste of ether, is to pour some of the thicker celloidin solution into a small cardboard box,—the lid of an ordinary cover-glass box serves the purpose admirably, place the tissue in this, and cover over with more celloidin.

It is now allowed to stand exposed to the air for a few minutes till the celloidin becomes somewhat firm, when it can be thrown into a mixture of alcohol and water, equal parts, or of the strength of 60 per cent. alcohol. When the celloidin has become quite firm round the tissue, the block can be cut out or turned out of the box, and for further use can be kept in alcohol of a similar strength. The *rationale* of the above proceedings will be at once apparent. It is necessary to have the tissue free from water, and, at the same time soaked in ether, before it is placed in the celloidin solution; hence the preliminary proceeding of soaking the tissue previously in alcohol and ether. Then, by placing it first in a thinner solution and afterwards in a thicker, we ensure that the celloidin reaches all parts of the tissue, a matter of importance when the tissue is delicate and all its parts require support. It is not only, however, for delicate tissues that this method of embedding recommends itself. Sometimes the tissue to be cut is so small or so thin that it becomes a matter of the greatest possible advantage to embed it in celloidin, by means of which each section is surrounded by a zone of celloidin which helps greatly in the after manipulation required.

In cutting the tissues so prepared, the so-called “dry” method of cutting sections must be employed, if we wish to obtain the full advantages of this method of embedding. Acquaintance with this method—comparatively speaking so seldom employed in this country—so impresses one with the advantages which in many cases it offers over the ordinary method by freezing so much in use at home, that one cannot but feel a certain sense of astonishment at the tenacity with which we in this country have retained our old methods long after they have been rejected by our friends abroad. The instrument which has been recently turned out by the Cambridge Scientific Company will, therefore, supply a want long felt by histologists in this

country. In Germany, the microtomes most in use are those made by Schanze, *mechaniker*, of the Pathological Institute in Leipzig, and by Jung, *mechaniker*, in Heidelberg. The latter often goes by the name of the "Heidelberg" instrument or the "Thoma" microtome. The principle of these instruments is sufficiently well known as to preclude any necessity on my part for a detailed description of their working. In both the tissue is made fast within a clamp, which moves, in the case of the Heidelberg instrument, along a finely inclined plane, in the Schanze microtome up a vertical plane, the movement in these planes being effected by a fine screw adjustment with millimetre scale, so that the thickness of each section can be accurately judged of and regulated. The knife, fixed on a heavy piece of steel, moves smoothly along a horizontal plane. In the Heidelberg instrument the screw adjustment is particularly fine, enabling one to cut sections of extreme thinness. In other respects, it is the instrument most suitable for cutting embryos an apparatus existing in it by means of which almost automatically all the sections can be made exactly of the same thickness. On the other hand, for general use the Schanze microtome will, in my opinion, be found the preferable one, especially if large sections be required, as of pons, medulla, &c., and it has the advantage of having a freezing apparatus in connection with it, worked by means of ether.¹

The tissue to be cut must as usual be well hardened. If it be of sufficiently firm consistence, *e.g.*, liver or kidney, sections may readily be obtained from it by simply fixing it in the clamp, wedged in between two pieces of hard waxy liver to give support. This is, however, at best but a rough method, and is not applicable to tissues of any delicacy. Much the better plan is, first of all, to fix the tissue to the top of a cork by means of a drop of gum; on throwing the cork into spirit, the gum soon becomes perfectly hard, and thus the tissue is securely held. In doing this, it is convenient to stick a small leaden pin into the under surface of the cork, the weight of which sinks the cork, and at the same time keeps the tissue uppermost. For cutting, then, the cork is made fast within the clamp, with the tissue

¹ The price of these instruments varies from £4 to £10, according to size and completeness.

securely attached to its upper surface. The surface of the tissue, as it is cut, is kept moist with spirit, this being applied by means of a camel's-hair brush, and the blade of the knife must also be kept wet; both objects being attainable by simply wetting the upper surface of the knife from time to time, the fluid passing from this on to the tissue each time the knife crosses it. The sections are transferred from the knife at once into methylated spirit, and after the desired number have been made, the cork with the tissue attached is thrown back into spirit till again required. No waste of tissue is involved by this method, a matter of no little importance, when, as occasionally happens, only a small piece is at our disposal; and its convenience in private working, where only a few sections at a time are required, is extremely great. The result stands in marked contrast with that obtained by the freezing method, where, each time that a few sections are required, the tissue must be steeped in water for a period of twelve to twenty-four hours to free it from spirit, and where, as a rule, the tissue must be cut completely at the time, as its subsequent use after being frozen is generally out of the question.

The tissue embedded in celloidin is also made fast to cork, but with celloidin instead of gum. This is done by placing it in some fluid celloidin on the top of the cork, and then pouring more celloidin over it. It is then allowed to stand exposed to the air till the celloidin solidifies, after which it is thrown back into a mixture of alcohol and water of the strength before mentioned. As the central portion of the celloidin remains longest fluid, air bubbles from the cork sometimes rise into it, and may interfere with the firmness of attachment. To prevent this occurrence it is advisable to have the corks previously steeped in alcohol and water. Sections can now be made of the tissue in the same way as before described.

It now remains to say something of the method of handling the sections so obtained. The celloidin cuts very easily and smoothly. For staining, the sections can be treated in the ordinary way. Each section of tissue is surrounded by a somewhat stiffish zone of celloidin, which renders the after manipulation of delicate tissues very easy. After being stained, the sections are washed out first in spirit, or water if required,

then transferred to alcohol. As previously mentioned, celloidin dissolves slowly in absolute alcohol, but for purposes of dehydration this action is too slow to be taken into consideration. They are then clarified—*not in oil of cloves*, which rapidly dissolves the celloidin but in origanum oil or xylol. The former is to be preferred; its odour is more pleasant than that of xylol, but more important is the fact that xylol is liable to cause the tissues to shrink up into folds which are difficult of removal. Origanum oil has no such effect. The celloidin now becomes perfectly transparent, almost invisible, and the section is mounted in Canada balsam. We must be very careful to have the section free from water before placing it in origanum oil, as the slightest trace of water makes the celloidin opaque, and some time is required in the origanum oil for this opacity to clear up.

I have sometimes, however, made use of clove oil for clarifying the tissues; under circumstances, viz., where the tissue has been embedded in celloidin to keep different portions of it together, rather than to give support to the individual tissues. In this way one has been enabled to keep the section intact during all the manipulations, and, then, at the last stage, after the section has been placed on the slide, by clarifying with oil of cloves, to remove at once all the celloidin and leave the tissue quite natural. In certain cases this method is convenient.

Such is the method of embedding in celloidin. After considerable experience now in its use, I can strongly recommend it as a most valuable adjunct to our resources in Histology. At the same time, it is far from my intention to advocate any one method of embedding or cutting to the exclusion of all others. No one can be blind to the advantages which the method by freezing offers in most cases. Where large numbers of sections have to be made, and where the amount of material at our disposal is great, the method of freezing will always recommend itself for its simplicity, its cheapness, and the rapidity with which sections can be made. Hence, for class-teaching purposes this method is by far the best. But where an exact study is to be made of some delicate organ or tissue, or where it is desirable to obtain sections of the whole tissue, the method of embedding in celloidin and the use of the

"dry method" of cutting sections, are greatly to be preferred, the advantages which they offer being readily appreciable on even a brief acquaintance.

Great as these advantages are, in suitable cases, they are even surpassed by those offered by another method of embedding, with which we have been long acquainted, viz., embedding in *paraffin*. Owing to the general use of the method of freezing for cutting sections, and its inapplicability to the cutting of tissues embedded in paraffin, this latter method has hitherto not been so extensively adopted as it really deserves to be, for it is certain that by no method yet known to us can such delicate sections of tissues be obtained as after embedding in paraffin, a fact evidently of the greatest importance to histologists, but whose importance has hitherto not been fully recognised. To be successful, however, in embedding in paraffin, a definite procedure must be followed, the object of which, briefly stated, is to free the piece of tissue from all traces of water before placing it in the paraffin itself. The following method will be found to give very good results:—To effect this dehydration, the tissue must lie for a certain time in absolute alcohol, from which it is transferred to clove oil, where it is allowed to remain till it becomes saturated with the oil, a stage generally indicated by the sinking of the tissue in the oil. To remove this oil, and at the same time to have the tissue soaked in some fluid in which paraffin is soluble, the tissue is next placed for 4–5 hrs. (a much shorter time will suffice if small pieces of tissue are to be embedded, viz., $\frac{1}{2}$ –1 hr. in xylol or turpentine) in xylol, at the end of which time it is ready to be placed in paraffin. But here, as with celloidin, we first use a weak solution, viz., equal parts of xylol and paraffin, maintained at the melting point over a water bath; in this the tissue is allowed to lie for $\frac{1}{2}$ hour, the dish being covered over during this time to prevent the evaporation of the xylol. It is then transferred to pure paraffin, maintained in a similar way at the melting point, where it is kept for 1–1 $\frac{1}{2}$ hrs., according to the size of the tissue, the dish now being left uncovered to allow all the xylol to evaporate. The tissue is then placed in a small paper boat, some of the fluid paraffin is poured over it, and the whole immediately floated on water to allow of rapid cooling. On cutting into the solidified

paraffin, the tissue will be found completely incorporated with it, and of a dark translucent colour, and in this encasing it can be preserved an indefinite length of time.

For purposes of cutting, the paraffin is made fast to a cork with the aid of a gentle heat, the surface of the cork being previously dipped in fluid paraffin, and sections are obtainable in the way already described. Sections of extreme delicacy can in this manner be obtained; if desired, not thicker than a single layer of cells, a result, when obtainable, which fully compensates for any labour expended in suitably preparing the tissue for section. Each section as it is made tends to roll up, an occurrence to be avoided, since otherwise the section is as good as lost. To prevent this, it is only necessary to touch the edge of the section with a fine brush immediately the knife enters the paraffin; the section then retains the "bent" thus given to it. If sections in series have to be obtained, they can be kept attached to each other in lines, like the segments of a tapeworm; hence this method of embedding and cutting is invaluable in embryology. In such cases, the rows of sections are transferred directly to a large slide capable of holding 20, 30, or even more sections, and are permanently fixed on the slide by gently pressing with the finger the sections against the slide, or merely touching them with alcohol. The sections are thoroughly clarified, at the same time that the paraffin is removed from them, by throwing the slide over night into xylol, after which they are covered with Canada balsam, and a large cover-glass is placed over the whole series. In this way, in the course of a very short time, we can obtain the 2000 or 3000 sections of an entire embryo in complete linear series, without trouble and without any risk to the sections, a result obtainable in no other way yet known to us. The great advantage of the method is, that all the necessary manipulation is carried out with the tissue as a whole, so that the process is in reality an extremely simple one, and any trouble which it involves is amply compensated for by the ease of manipulation of the sections afterwards. Oil of turpentine can be used instead of xylol in embedding the tissue, as also in removing the paraffin afterwards, but the latter, when obtainable, is in my opinion to be preferred, as its solvent action on paraffin is almost instantaneous.

As to the *staining* of tissues embedded in paraffin, two plans may be followed. In embryology, our procedure is much simplified by staining the embryo entire before it is embedded. An extremely good staining agent for this purpose is *alum carmine*. This is made by adding 1 gramme pure carmine to 100 c.c. of a warm 5 per cent. solution of alum, then boiling for twenty minutes, and filtering the solution after cooling. This is a very pretty staining agent. It stains quickly, but has the great advantage of not readily overstaining. Sections can be left in it from ten minutes up to twenty-four hours without becoming overstained. It is generally convenient to leave the sections in the fluid over night, but if necessary ten to twenty minutes will usually suffice. An embryo must be left in for twelve to twenty-four hours. In the second place, it is very clean to work with; the tissue seems not to take up any excess of the stain, and hence the washing out in water can be completed in a few minutes, in which respect it stands in marked contrast with gentian violet, which stains very deeply. If an embryo has been stained in alum carmine, it is necessary to allow it to lie in water for about twelve hours, changing the water two or three times during this period. The resulting staining is limited for the most part to the nuclei, the colour partaking more of the purplish tint of hæmatoxylin than the reddish of carmine. It is necessary to have the embryo free from alcohol before placing it in the alum carmine, but, after it has been stained and washed in water, it can be placed in alcohol and embedded in the usual way in paraffin. The sections, therefore, on being cut are ready at once for mounting without further manipulation, and this is done in the way already described.

If the tissue cannot be stained *en masse*, the second of the two plans must be adopted. The sections, as made, are either fixed directly on the slide in the way already mentioned, or they are placed at once in xylol or turpentine. In the former case, the sections being permanently fixed to the slide are freed from paraffin by pouring some xylol over them. Before staining them, we wash out the xylol by passing a few drops of alcohol over them, and then, after dipping the slide in water, we stain the sections by placing a few drops of the staining fluid on the slide and allowing it to remain for a sufficient length of time.

The slide is then dipped in water, the sections dehydrated in alcohol, clarified in oil of cloves or xylol, and finally mounted in Canada balsam. The ease with which all this, apparently complicated, procedure can be carried out is very great. It is to be remembered that our sections are probably extremely thin, consisting perhaps of a single layer of cells; but they are permanently fixed to the slide, a number of them being on one slide, and hence they run no risk of being torn during all the subsequent procedure, and we are dealing, not with one, but with a number of sections at the same time.

If the sections have been placed in xylol or turpentine, and completely freed from all remains of paraffin, they can be kept in alcohol, and used in the ordinary way for purposes of staining, &c.

In conclusion, if one were to institute a comparison between the relative merits of these two embedding agents, celloidin and paraffin, one could only remark, that for general purposes, the celloidin will be found more generally useful than the paraffin, and especially in the study of the spinal cord, medulla and pons, and nervous tissues generally; but that for fine histological observation, as well as for embryological purposes, the method of embedding in paraffin is by far our best in histology, and gives results which can in no way be equalled by any other method yet known to us.

THE SACRAL INDEX IN VARIOUS RACES OF MANKIND. BY Professor WILLIAM TURNER, M.B., F.R.S.

IN my paper on "The Index of the Pelvic Brim as a basis of Classification," published in the October number of this *Journal* (1885), I briefly referred to variations in the relative length and breadth of the sacrum in different races of men, and pointed out that in some races the length exceeded the breadth, and that in others an opposite relation prevailed. These differences may be expressed numerically by computing a sacral index by multiplying the breadth of the sacrum by 100 and dividing by the length. When the sacral index is above 100 the breadth of the bone is greater than its length; when the index is below 100 the sacrum is longer than broad. The following descriptive terms may conveniently express these differences in the relative length and breadth of the sacrum. As the Greek word *ῥεπὸν* is the equivalent of the Latin *sacrum*; the term *dolichohieric* would signify a sacrum in which the length exceeded the breadth, whilst *platyhieric* would signify a sacrum in which the breadth exceeded the length.

In considering the modifications in the sacral index, as in the index of the pelvic brim, it is important to bear in mind that sex modifies the relative proportions, and that in women the sacrum as a rule is broader in proportion to its length than in men.

In working out the results at which I have arrived, I have measured a number of original skeletons, a few of which were brought home by H.M.S. Challenger, but the greater number of which are in the Anatomical Museum of the University of Edinburgh. The detailed measurements of these skeletons are given in the Tables in Part II. of my Report on the Human Skeletons now in type for the Challenger Reports. I have also examined the literature of the subject, so far as I have had access to it, and have analysed the observations on the length and breadth of the sacrum recorded by previous observers.

Amongst Europeans M. Verneau has given, in sixty-three men, the mean length of the sacrum as 105 mm. and the mean breadth at the base as 118 mm., and in thirty-five women the mean length as 101

mm. and the mean breadth as 116 mm. If an index be computed from these figures the males will be found to possess a sacral index of 112·4 and the females one of 114·8. From Görtz's measurements of the length and breadth of the sacrum in European women I have calculated an index of 118·9. Dr Garson gives 101 mm. as the mean length of the sacrum in fourteen European women, and the mean breadth as 118·3, which yield an index of 116·8, slightly higher than that furnished by M. Verneau's measurements, but not so high as those of Görtz. But from Carl Martin's measurements of sixteen pelves, presumably German, the sacral length was 100 mm., the breadth 105 mm., and the index therefore only 105. In Europeans, therefore, both males and females, the sacrum had a decidedly greater diameter at its base than in its long axis, or, in other words, it was platyhieric.

In the Australians, again, an opposite relation prevails. In only one of the six adult males measured in Table I. was the breadth of the sacrum at the base greater than its length, in two these diameters were equal, and in the remaining three the length exceeded the breadth. The mean sacral index, therefore, of the males was only 98, and in the single adult female this index was only 101. In a male measured by Keferstein the index was 88, in one by Barnard Davis 90, and in five males measured by Spengel it was 111, 106, 97, 89, and 111 respectively. In the single male Australian measured by Verneau the sacral breadth at the base is stated to be 105 mm. and the length only 87 mm.; but the latter diameter is so small for an adult male of this race, that one is disposed to think there must be either some error in the table or that the sacrum could not have been normal: the index furnished by these measurements, 120, is therefore exceptionally high. The sacral index of a female measured by Barnard Davis was 89, and the mean index computed from the two females measured by Verneau was 105·9, and the mean sacral index of the five women measured by Garson was 114. Excluding, therefore, M. Verneau's male pelvis for the reason given above, it is clear that in the Australian men the breadth of the sacrum was small in relation to its length, so that in a considerable proportion the index did not exceed 100, and the mean of the thirteen males was 98·5, *i.e.*, they were dolichohieric. In the women, again, the sacrum was relatively broader than long, though it did not attain the proportions reached in the European, for if we take the mean of the nine female pelves measured by B. Davis, Verneau, Garson, and myself, the sacral index was only 102·5.

The proportions of the sacrum have been recorded in two Bushmen by G. Fritsch; in the one the length was 95 mm. and the breadth 91 mm., the sacral index being 95·8, in the other¹ the length was 94 mm. and the breadth 83 mm., the sacral index being 88. These two specimens, conjoined with the male measured in Table VI. in my Challenger Report, give the mean sacral index of three males as 94.

¹ This Bushman pelvis has had some of its characters described by Johannes Müller.

Verneau's two Bushwomen had a mean sacral index 100; Görtz's Bushwoman, Afandy, had a sacrum 87 mm. long and 90 mm. broad, the index being 103; whilst in an adult female recorded by G. Fritsch the sacral length was 97 mm. and the breadth 79 mm., the index being only 81. The mean of these four specimens was 94·7. There can, I think, be little doubt that it is the rule in the Bush race for the male sacrum to be longer than broad, *i.e.*, dolichohieric. It is not, however, quite so clear as to the relative proportion in the female, for although the mean of the four specimens is only 94·7, yet it will be observed that this low index is due to one of the specimens being only 81.

G. Fritsch has also recorded the sacral length and breadth in the pelves of some Hottentots and Kaffirs from which indices may be computed. In a Hottentot woman the length of the sacrum was 95 mm., its breadth at the base 81 mm., and its index was 85. In one male Korana Hottentot the sacral length was 95 mm., the breadth 90 mm., and the index 94·7; in another the length was 105 mm., the breadth 79 mm., and the index only 75. In Wyman's male Hottentot the sacral index was only 82. In all these specimens, therefore, the length of the sacrum exceeded the breadth, and the mean index of three males was 83·9. In the six male Kaffirs measured by Fritsch the highest sacral index was computed to be 106 and the lowest 82, the mean of the series being 92·8. In the single female the sacral length was 86 mm., the breadth 92 mm., and the index 107. In the male Kaffirs, therefore, the sacrum is as a rule longer than broad, and both in them and in the Hottentots it is dolichohieric.

In all the Negro pelves measured in my Table III. the breadth of the sacrum exceeded the length, and the mean sacral index of the four males was 114; but though in one of the Negresses the sacrum was longer than broad, in the other the relation was reversed, and the mean index in the two specimens was only 99. In one of Spengel's male Negros the sacral index was 114, in the other 97; whilst in a Negro from the Gaboon measured by Barnard Davis it was only 87. If we take, however, the series of twenty-two males described by M. Verneau from Guadeloupe, Mozambique, Nubia, or of unknown locality, the proportions are such as to give a mean sacral index of 97, whilst the seven females either from Guadeloupe or an unknown locality had a mean sacral index 105·5. In the Negress measured by G. Fritsch the sacral length was 93 mm., the breadth 86 mm., and the index 92. The mean of the twenty-nine males measured by Verneau, Spengel, B. Davis, and myself gave a sacral index 106, *i.e.*, they were platyhieric. The mean of the ten females measured by Verneau, Fritsch, and myself was only 98·8; so far, therefore, as these specimens show, in the Negro race the sacrum presents the exceptional arrangement of being in the female not so broad in proportion to its length as in the male.

In the only male adult Andaman Islander, as well as in the three adult females in my Table IV., the breadth of the sacrum exceeded the length; the sacral index of the adult male was 114, that of a young male was 106; the mean index of the three adult females was 111,

and the index of a young female was 96.5. In the series of eight male Andamanese measured by Professor Flower the mean sacral length was 97.1 mm. and the mean width was 91.3 mm., the index being 94, and in the series of nine females the mean length of this bone was 89.7 mm. and the mean breadth was 95.2 mm., the index being 106. In the single male specimen described by Barnard Davis the sacral breadth was so much less than the length that the index was only 77. It is clear, therefore, that the high sacral index in my male pelvis was an individual peculiarity, and that it is the rule in the male Andamanese for the length to exceed the breadth, so that the sacrum is dolichohieric.

In Fritsch's Nikobar Islander the sacral length was 101 mm. and the breadth was 90 mm., the index therefore being 89, or dolichohieric.

The three male Tasmanians measured by Barnard Davis had a sacral index respectively 92, 86, 114, giving a mean of 97, so that the sacrum was dolichohieric; but in the single female the index was 104.

In each of my five female pelvises from Oahu, Sandwich Islands, the sacral breadth exceeded the length, and the mean index was 113, and in the Tongan Islander the index was 115. In M. Verneau's two Sandwich Island men the mean sacral index was also 113, and in his male Tongan it was 100. In his male Mangarevan the sacral index was 100.9, and in his Noukahivan it was 99. In Barnard Davis's male Tannese this index was 100. In each of my two male New Zealanders the sacral index was 96. In Verneau's Loyalty Islander the sacral index was 107.7, and in Barnard Davis's male it was 103. In Verneau's series of New Caledonians the mean sacral index in the males was 102 and in the females 120, and in his single male New Guinea specimen it was 111.6. It is clear, therefore, that in the pelvis of these Pacific Islanders, of both sexes, whether we regard them as pure Melanesians or pure Polynesians, or as a mixture of the two races, the sacral breadth is as a rule greater than the length and the proportions of that bone are platyhieric.

In my two male Guanche pelvises the mean sacral index was 108.5, and in M. Verneau's male this index was 102. In my male Esquimaux the sacrum had the abnormal index 139, whilst this index in the female was 106. In my male Laplander the sacral index was 106, in the female 112; but the mean index in M. Verneau's two male Lapps was only 92.6. The number of pelvises in the Guanche, Esquimaux, and Laplanders is too small to form an average, but I think it not unlikely it will be found, both in the Guanche and the Esquimaux, that it is the rule for the sacrum to be broader than long.

Of the natives of India the sacral index of the male Hindoo in my Table V. was 109. The dimensions of the sacrum in a male Hindoo presented to the museum by Dr. Anderson were—length 110 mm., breadth 122 mm., the index being 111; in the female Hindoo the index was 127. In all, therefore, the sacrum was platyhieric. In my Sikh the sacral index was 124.5, but in a male Sikh measured by Barnard Davis this index was only 91. In a male Bhutea, also measured by B. Davis, the sacral index was 93.6.

The Chinese measured in my Table V. had a sacral index 98. In von Franque's female specimen the length and breadth of the sacrum were equal at 111 mm., and the index was therefore 100. In Verneau's female pelvis the sacral index was 120, but in his male, owing to the great length of the sacrum, 134 mm.,¹ this index was only 78. In Spengel's male the sacrum had a still greater length, 139 mm., and its breadth was 108 mm., the index being 77·7. Owing to the paucity of the specimens, and the wide diversity in the relative proportions of this bone in the pelves measured, it would be difficult to state, even approximately, the mean sacral index; but from the information at present before one it would seem as if in the male Chinese the length of the sacrum may exceed the breadth, though the possibility of Verneau having included the sixth vertebra in his measurements is not to be lost sight of. In Verneau's male Annamite also the sacral index was only 87·5.

The female Aïno in the Barnard Davis collection had a sacral index 91; whilst in the male Aïno, measured by Scheube, the length and breadth of this bone were equal at 115 mm. and the sacral index was 100.

In my male Malay the sacral index was 95. In von Franque's female the sacral length was 102 mm. and the breadth 100 mm., the index being therefore 98. In Barnard Davis's two male Javanese the sacral index was respectively 96 and 88, but in Verneau's female, owing to the remarkable shortness of the sacrum, 72 mm., this index rose to 145. Of the twenty-six Javanese female pelves measured in Zaaïjer's Table I., the length of the sacrum exceeded the breadth in eleven specimens, it was less than the breadth in fourteen specimens, and in one of these the two dimensions were equal. As in the female pelvis it is the rule for the sacrum to be relatively broader than in the male, there can, I think, be little doubt that, in the Malay race, the male sacrum is longer than it is broad, and that this bone is dolichohieric.

Of the North American Indians von Franque gives the length of the sacrum in the male Flathead at 112 mm. and the breadth at 114 mm., the index being 101·8; whilst in the female the length was 107 mm. and the breadth 108 mm., the index being 100·9. In Barnard Davis's male Illinois Indian the sacral index was 115·8, and in Verneau's female Mexican it was 108. Probably, therefore, in the North American aborigines the average breadth of the sacrum is more than the average length.

The dimensions of the sacrum have been recorded in a few more specimens of South than of North American Indians. In a male Puelche measured by Barnard Davis the sacral index was 95·8, and in a male ancient Peruvian it was 92. From Verneau's table of sacral

¹ Verneau states that in the Annamite and male and female Chinese pelves the sacrum consists of six pieces. The Chinese woman, notwithstanding this, has a relatively broad sacrum; but if he has included the sixth piece in his measurements of the Chinese man and of the Annamite the low sacral index is accounted for. It is not unlikely that Spengel's specimen may have had a similar arrangement.

measurements I have computed the sacral index in a male Charruan at 108, in a male Botocudon 117, in a male Bolivian 93, the mean of two male Peruvians 128, in a male Goytacazen 119; whilst the mean of three female Peruvians was 121·7, and in a female Goytacazen it was 110·5. Of the eight males three had a sacral index below 100, but the others were so much above 100 that the mean sacral index of the series was 107·5, and the mean of the four females was 116. The measurements recorded by J. G. Garson, of four male Yahgans from Tierra del Fuego, gave a mean sacral length 103·2 mm., and a mean sacral breadth 112·2 mm., the mean index being 109, and in each specimen the index was above 100. In the South American Indians, therefore, I have little doubt that the mean breadth of the sacrum exceeds the mean length, so that the aborigines in both the north and south of that continent are platyhieric.

From this analysis of my own measurements and of those of other anatomists it is clear that the proportion of the length to the breadth of the sacrum varies in different races of mankind. In some it is the rule to find it longer than broad, in others broader than long. Although additional observations are still greatly needed, especially on some of the races, yet it seems possible to make a provisional arrangement of the races of men into two groups, according as the sacral index is below or above 100, and in this Table, as in the one given in my previous paper, "On the Index of the Pelvic Brim," the proportions are estimated on the measurements in the male sex.

DOLICHOHIERIC.	PLATYHIERIC.
<i>Sacral Index below 100.</i>	<i>Sacral Index above 100.</i>
Australians	Europeans
Bushmen	Negros
Hottentots	Melanesians
Kaffirs	Polynesians
Andamanese	Hindoos
Tasmanians	Guanche?
Chinese?	Esquimaux?
Aino?	North American Indians
Malays	South American Indians

A comparison of this Table with that framed on the index of the pelvic brim will show that in many instances a dolichopellic brim is conjoined with a dolichohieric sacrum. For example, this is the case in the Australians, Bushmen, Kaffirs, Andamanese, Ainos, and Malays. Again a platypellic brim is conjoined with a platyhieric sacrum in the Europeans, American Indians, and probably the Guanches and the Esquimaux. The pelves which I have arranged in the mesatipellic, or intermediate division, partly belong, as regards the proportions of the sacrum, as in the Negros and Melanesians, to the platyhieric group, and partly, as in the Tasmanians, to the dolichohieric group. As the width of the pelvic brim is materially influenced by the breadth of the sacrum, it was to be expected that a platypellic pelvis would have

a relatively wide sacrum, and that a dolichopellic pelvis would have a relatively long sacrum. There are two races which, however, have an anomalous position in these two tables, viz., the Chinese and the Polynesians. The Chinese with a platypellic brim, it will be observed, are placed with pelves in which the sacrum is longer than broad. The position, however, which the Chinese occupy in this table can only be regarded as provisional, and when a larger series is examined, on the basis of only five sacral vertebræ being measured, it is not unlikely that their position in the table of sacral proportions will have to be altered. The position of the Polynesians in the table in the preceding paper is also provisional, as a wider series of observations may require them to be transferred to another column in that table.

In connection with the relative dimensions of the conjugate and transverse diameters of the pelvic brim, and those of the length and breadth of the sacrum in the different races of men, a few words may appropriately be written on the corresponding relations in the pelvis in other mammals, at least in those which possess five vertebræ in the sacrum. In the Anthropoid Apes the length of the sacrum is considerably greater than its breadth. In two oranges, which I have measured, the mean sacral index was 87; in two chimpanzees the mean was 77, and in a gorilla the index was 72; in an ox the sacral index was 87, and the sacrum in all these was markedly dolichohieric. The mean index of the pelvic brim in two chimpanzees was 133; and in an ox the pelvic index was 110. In these animals the conjugate diameter of the pelvic brim was materially greater than the transverse, i.e., the index was dolichopellic. When a human pelvis therefore is dolichopellic, and has also a dolichohieric sacrum, it corresponds in both characters with the more usual type of mammalian pelvis; and, as compared with the relations of parts met with in the Europeans, it possesses a degraded or animalised arrangement.

THE BLOOD-FORMING ORGANS AND BLOOD-FORMATION: AN EXPERIMENTAL RESEARCH. By JOHN LOCKHART GIBSON, M.D., *formerly Senior Demonstrator of Physiology, University of Edinburgh.*

(Continued from p. 113, vol. xx.)

PART II.—ON THE BLOOD-FORMING ORGANS.

HAVING reviewed the different elements found in the blood, I now pass on to ascertain, if possible, the function of the so-called *blood-forming organs*.

In considering blood-formation, I restrict myself entirely to blood-formation in extra-uterine life.

The organs called "blood-forming" are the spleen, lymph-glands, bone-marrow, and thyroid gland. I have endeavoured experimentally to discover if all of these organs produce red blood-corpuscles in extra-uterine life, and which of them are most active. That they all, with the exception of the thyroid, produce white blood-corpuscles, I think nobody will doubt.

With regard to the formation of red corpuscles in extra-uterine life, the greater number of recent authors (Neumann, Bizzozero, &c.) have given the *bone-marrow* the first place as a producer of red corpuscles in extra-uterine life; though some authors deny that it has any blood-forming action. A smaller number (Rindfleisch, &c.) have given the *spleen* the first place; a much larger number giving it a second place, and a few (Neumann and Ehrlich) giving it no place at all. A still smaller number (Zesas and Credé) look on the *spleen* and *thyroid* together as the chief producers of red corpuscles; others denying to the thyroid any blood-forming action. The *lymphatic glands* receive, here and there, a little irregular and indefinite support.

The points which seemed to me most doubtful, because differed about by men generally recognised as the most competent authorities on the blood and on blood-formation, were:—*1st*, how the red corpuscles are produced in extra-uterine life; *2nd*, whether the spleen has any activity as a red-corpuscle-forming gland in

extra-uterine life; *3rd*, whether the lymphatic glands have any activity as producers of red blood-corpuscles; and *4th*, whether the thyroid gland has any blood-forming function.

I shall consider—*firstly*, the results of excision of the human spleen, and what can be learnt from the recorded cases, with regard to its blood-forming function; *secondly*, the experiments and results of the principal observers who have excised the spleen from animals and watched the effect; and *thirdly*, my own experiments on the function of the spleen, as also on the function of the lymphatic glands. The function of the bone-marrow will be considered together with the function of the spleen.

The consideration of the thyroid gland will be more conveniently left until the consideration of the spleen is completed, as I have been unable to find any grounds for supporting a blood-forming action of the thyroid.

It has very recently been said that we do not know much more about the spleen than Aristotle did when he said: "The spleen is not an organ which is indispensably necessary to the body;" and that we may still call it, as Galen did, the "organ full of mystery." This, however, is hardly true. For although there is still but little uniformity of opinion as to the function of the spleen, yet much light has of late been thrown on the subject, more especially by the very able researches of Bizzozero. And I think that if it can here be shown that the spleen is an organ with an important action in the regeneration of the blood after hæmorrhage, a function will be given it not unworthy even of an organ of its considerable size.

As early as 1549 the spleen was successfully removed from a human subject;¹ and previous to that date it had been ascertained that spleenless dogs not only lived after the operation, but even seemed to thrive and grow fatter.

Chronological lists of excisions of the spleen in man are given by Crédé² and Zesas.³ Crédé's paper gives a list of thirty

¹ Fioravanti, *Del tesoro della vita humana*, libr. ii. cap. 8. (Fioravanti was the physician of the case, Zaccarelli the surgeon.)

² B. Crédé, "Ueber die Exstirpation der kranken Milz beim Menschen," *Arch. f. klin. Chir.* (v. Langenbeck's), Bd. xxviii. (1882), pp. 401-410.

³ Zesas, "Ueber Exstirpation der Milz am Menschen und Thiere," *Arch. f. klin. Chir.*, Bd. xxviii. (1882), pp. 157-178.

excisions of the diseased spleen, and also considers what has been learnt from the cases with regard to the blood-forming function of the spleen. Zesas, besides considering those cases where excision was performed for enlargement of the spleen, gives the results of twenty cases collected by him of excision of the spleen after penetrating wounds of the abdomen with injury to the spleen. Among these twenty cases Zesas could not find a single fatal result.

Of the thirty cases quoted by Crédé, sixteen were in leukæmic patients, all of whom died during or shortly after the operation. From these sixteen nothing can be learnt regarding the function of the spleen, as the patients did not live long enough. Nor from them can we even conclude that excision of the spleen in leukæmia is in itself necessarily fatal. For the patients were presumably not operated on till after all other remedies had been found powerless, and therefore not till the disease was far advanced, and their vital resistance reduced to a minimum.

Of the fourteen other cases, five resulted fatally and nine were successful. Of the five unsuccessful cases two may be excluded. In one, where death occurred six hours after the operation, the ligature was found compressing the tail of the pancreas. The patient, who before the operation was in a very feeble condition, died of shock. In another, where death occurred two hours after the operation, 1½ lbs. of blood was found in the abdomen. Neither of these cases can, in my opinion, have their fatal termination ascribed to the absence, or, indeed, even to the removal, of the spleen.

We have left, then, three fatal cases out of twelve; which cannot be called a large mortality for such an operation, especially as so many of the operations were performed before attention was drawn to the immense importance of antiseptic precautions during operations on the abdomen.

The information which can be gathered from these recorded cases with regard to the blood-forming action of the spleen is not very definite, but is still of value. The blood seems to have been examined after the operation in only five of the cases:—

1. and 2. Two cases of Péan,¹ where some weeks after the operation there was a slight increase in the relative number of white corpuscles as compared with the red.

3. Czerny records a case in which up to five weeks after the operation there was apparently no change in the blood. The blood was not examined later. In this case the cervical and inguinal glands were painful for several weeks after the operation.

4. Martin records a successful case where examination of the blood yielded negative results.

5. By far the most carefully recorded case, however, is by Crédé, in the above-mentioned paper. In it the changes in the blood seem to have been of a marked character. Two months after the operation (which was for a cyst of the spleen) the alteration of the blood was at its height, and the proportion of white to red corpuscles was

¹ Péan, *Tumeurs de l'abdomen*.

1 : 3 or 4. "There were also a great number of small red corpuscles (Mikrozyten), some of them nucleated." The blood gradually changed back to normal again, and was quite normal $4\frac{1}{2}$ months after the operation. Four weeks after the operation a painful swelling of the whole thyroid gland appeared, which lasted for four months, disappearing soon after the blood resumed its normal condition. There was "neither swelling of the lymph-glands nor pain in the bone-marrow." The patient was a man of 44 years, and he recovered his health entirely, so that he was able to continue his work, that of a mason.

I was fortunate enough to hear Dr Credé's son speak of the case at the Berlin Surgical Congress this year. The man was quite well, three years after the operation; and the white corpuscles had sunk *below* the normal number. Credé mentions particularly that the marked changes in the blood of his patient were not seen for some weeks after the operation, and that he did not find a return to a normal condition until four months after it; and says that the four other cases were not examined after they left their respective hospitals, four or five weeks after the operation, whereas he watched the blood of his patient for ten months. He thinks it possible that in the blood of the other patients, more especially of those of Péan, there may have been changes which were not marked until after the patients left the hospital, and therefore until observations on the blood had ceased to be taken. From these five cases, Credé gathers that the spleen has an important action in turning white into red corpuscles; that when the spleen is removed the retrogressive metamorphosis of the red corpuscles diminishes; and that the white corpuscles increase in number until another organ takes on itself the function of turning them into red ones. And this other organ may, he says, "possibly be the thyroid gland." He believes that the lymph-glands carry on their function as before, and sees no reason why they should increase in size. "The bone-marrow," he says, "which in normal conditions produces only a very moderate number of small red corpuscles, appears to increase its function after the spleen is removed." He gives his conclusions in the following tabulated form, and supports them by his own case and the two cases of Péan, and also by Zesas' observations on animals, to be afterwards mentioned:—

1. "The adult human subject bears the removal of the spleen without injurious effect.

2. "The removal of the spleen causes changes in the condition of the blood, which afterwards pass off.

3. "These changes are overcome by increased activity of the thyroid gland and the bone-marrow.

4. "The spleen changes white corpuscles into red."

I have given these conclusions of Credé's before going further, because they are the results of observations on the human subject, which of course are of much more value than similar observations on animals. Credé's own case is, however, the

only one which has been at all satisfactorily observed; and if we wish to know anything more definite with regard to the function of the spleen, we must pass to experiments on animals.

From the time when Kölliker¹ found nucleated red cells in the spleen during intra-uterine life and after a year of extra-uterine life, and therefore stated that the spleen is a blood-forming organ, blood-formation was pretty generally believed to be at least one of its functions, until Neumann² in 1869 cast discredit on this belief by saying that the blood-forming function of the spleen could not be demonstrated.

In his paper Neumann supports and extends the observations he made on the bone-marrow in 1868³, when he found that the red marrow contained nucleated red corpuscles at all periods of life. He considers that the red bone-marrow is throughout the whole of extra-uterine life the only producer of nucleated red corpuscles, and therefore of non-nucleated red corpuscles, and that after birth the spleen has no blood-forming function whatever; and he even expresses doubt about the spleen having a blood-forming function in the fetus. He says that the nucleated red corpuscles found in the spleen were just caught there as they were flowing through it in the circulating blood.

Freyer,⁴ a pupil of Neumann, found that the blood of the aorta was not poorer in nucleated red corpuscles than the blood in the spleen. He next attempted, by producing artificial anæmia in rabbits, to see if more such cells could be found in the spleen; and obtained a negative result.

In 1877 some valuable observations on the bone-marrow were made by Litten and Orth.⁵ These observations were rather in favour of Neumann's views, and at any rate gave further proof of the important part the bone-marrow plays in the formation of red blood-corpuscles. They found that the marrow in the shafts of the long bones was fatty, and that only the marrow in the spongy parts of the bones was functional in the direction of producing nucleated red corpuscles. They tried, by producing artificial anæmia in animals, to ascertain whether the fatty marrow also then became functional, to meet the increased

¹ Kölliker, *Handbuch der Gewebelehre*. [In the statement about Kölliker on page 101 of this volume (page 4 of reprint), the reader will please to put "spleen" instead of "liver," and in the footnote put "*Handb. d. Gewebelehre*," instead of "*Mikrosk. Anat.*, Bd. ii. p. 590." The need for this correction is the fault, not of Dr Gibson, but of a reviser in his absence.]

² Neumann, "Ueber die Bedeutung des Knochenmarkes für die Blutbildung," *Arch. d. Heilk.*, x. (1869), p. 68.

³ Neumann, *Centralblatt f. d. med. Wiss.*, 1868, No. 44.

⁴ Freyer, *Ueber die Betheiligung der Milz bei der Entwicklung der rothen Blutkörperchen*, Königsberg, 1872.

⁵ Litten and Orth, *Berliner klinische Wochenschrift*, 1877, No. 51.

requirements; and they found that the fatty marrow in the shafts of the long bones became red marrow, and was crowded with nucleated red corpuscles.

Professor Bizzozero and Dr G. Salvioli of Turin then set themselves the question:—Does the spleen, which is at any rate said to produce nucleated red corpuscles at the beginning of extra-uterine life, renew its former function, and, like the fatty marrow, again produce nucleated red corpuscles, when artificial anæmia is produced, and when therefore the reserve blood-forming capabilities of an animal are called into play? After elaborate researches, they found themselves able to give an affirmative answer to this question.¹

Their first step was to examine the spleens of healthy animals (they used dogs, guinea-pigs, and rabbits), in order to see whether they already contained nucleated red corpuscles.

They found, like Kölliker, nucleated red corpuscles in the spleens of *new-born dogs*; and even found them in one dog which was certainly more than a year old. In the spleens of *adult dogs*, such corpuscles were, as a rule, not to be found; although single examples could be found by diligent search.

In *young guinea-pigs*, numerous nucleated red corpuscles were found in the spleen. In *adults*, few were to be found; but they were very seldom entirely wanting.

In *rabbits*, they found these cells only very seldom after birth; while in the later period of youth and in adults they never found them. They therefore considered that the spleens of rabbits were peculiar after birth, in not containing any of these nucleated red cells.

Their second step was to produce artificial anæmia in animals and notice the effect on the spleen.

For the purpose of estimating the amount of anæmia, they employed the chromocytometer described by Bizzozero.² They obtained positive results only in *dogs* and *guinea-pigs*. Finding their results from *rabbits* negative, they decided to discontinue their observations on these animals.

Their first series of experiments was on *guinea-pigs*. They produced artificial anæmia in five guinea-pigs, by removing 1 to 2 per cent. (once 3 per cent.) of the body-weight of blood at a time. They never drew blood more than twice from the same animal; and the second blood-letting was always after an interval of three days from the first. Three days after the second blood-letting, *i.e.*, six days after the first, they killed the animal, and examined the spleen. In all cases the hæmoglobin of the blood on the day of death was between 50 and 60 per cent. of its original amount.

In all cases the *spleen* was found swollen and rich in blood, sometimes very much so, and always soft. It always contained "very numerous" nucleated red corpuscles.

¹ Bizzozero and Salvioli, "Beiträge zur Hämatologie," *Moleschott's Untersuchungen*, Bd. xii. (1881).

² Bizzozero, "Il cromocitometro, nuovo strumento per dosare l'emoglobina del sangue," *Accademia delle scienze de Torino*, 1879.

The *marrow* of the ribs and long bones also contained very numerous nucleated red corpuscles, sometimes more than the spleen.

Having obtained such distinct results with guinea-pigs, they next treated a series of ten dogs in exactly the same way. They sometimes drew blood as often as four times from a dog, the amount of blood drawn at each time varying from $1\frac{1}{2}$ to $3\frac{1}{2}$ per cent. of the body-weight. About three days after the last blood-letting the animal was killed. The percentage of hæmoglobin contained in the blood of the different animals on the day of death varied between 45 and 55 per cent. of its original amount.

They constantly found the *marrow* of the ribs very rich in nucleated red corpuscles, the marrow of the long bones being less rich in them.

In only one case (where there was only one blood-letting, and where the hæmoglobin was reduced only to 62 per cent.) did they fail to find nucleated red corpuscles in the *spleen*. In two cases they found a few, in three cases moderate numbers, and in four cases a great number. The spleen as a rule was slightly swollen; and in those cases where it contained numerous nucleated red corpuscles it was very much swollen, and very soft. As a rule the marrow of the ribs contained more nucleated red corpuscles than the spleen: only in one case is it remarked that it contained a similar number, viz., in a dog which had been rendered more anæmic than the others, the hæmoglobin having been reduced to 25 per cent. They describe the naked-eye appearances of the spleen as very characteristic: in fact, as so much so, that by simply looking at it they could say, "there will be nucleated red cells here." They describe it as "rose coloured and very much swollen," and as contrasting very distinctly with the spleens of normal dogs, which are generally very poor in pulp.

Their next step was to examine the blood of the splenic artery and the blood of the splenic vein:—

1st, To ascertain whether the vein contained more red corpuscles than the artery. 2nd, To ascertain the number of white corpuscles in the splenic vein relatively to the number of red corpuscles, and to contrast this relationship with the relationship in the splenic artery.

For this purpose they chose animals which had been rendered anæmic by blood-letting, and whose spleens were therefore in a state of activity. In two cases they used very young dogs without producing anæmia, as they knew from previous observations that the spleens of such dogs are still active.

The results they obtained were: that the blood in the splenic vein is richer in hæmoglobin than the blood in the splenic artery, and that the relative number of white corpuscles, as compared with the red, is greater in the splenic vein than in the splenic artery.

From these data, Bizzozero and Salvioli come to the conclusion that, as the only way in which the blood of the splenic vein can be richer in hæmoglobin than the blood in the splenic artery is by its containing a larger number of red corpuscles, therefore the blood of the splenic vein contains more red corpuscles than the blood of the splenic artery; and as they found the number of white corpuscles greater in proportion to the red corpuscles in the splenic vein than in

the splenic artery, they concluded that the addition of white corpuscles to the blood in its passage through the spleen is relatively still greater than the addition of red corpuscles.

They did not count the absolute number either of red or of white corpuscles in a given quantity of blood, but used the old, and, according to them, most accurate method of ascertaining the relative number of red and white corpuscles, viz., that of mixing a drop of blood with a drop of a .75 per cent. solution of common salt, so putting on a cover-glass as to obtain only one layer of corpuscles, and then through an eye-piece micrometer divided into squares counting all the red and all the white corpuscles in a square, and so obtaining their relative numbers.

They base their assumption that the hæmoglobin of the blood can be increased only by the presence of an increased number of red corpuscles on the observations of Welcker, Vierordt, Heidenhain, Panum, and others, who demonstrated that after blood-letting the hæmoglobin of the blood falls in percentage amount in consequence of the absorption of fluid plasma from the tissues; and on confirmatory observations conducted by themselves, and published in *Moleschott's Untersuchungen*.¹

By the observations last referred to, Bizzozero and Salvioli show that the fluid is not absorbed from the tissues at once, but that a time varying from six to forty-eight hours is required, before the amount of fluid necessary to replace the lost volume of blood has been absorbed, and accordingly before the hæmoglobin in the blood has reached its minimum. They further show that the diminution of hæmoglobin has a direct and constant relation to the amount of blood lost. For every per cent. of body-weight lost, there was a diminution of 11.14 per cent. of the hæmoglobin of the blood. This proportion they established after experiments on a great number of animals.

If these results of Bizzozero and Salvioli are compared with the results of J. F. Lyon,² who produced artificial anæmia in animals and counted the number of red corpuscles in the blood on the subsequent days until regeneration had occurred, it will be seen that the time when the number of red corpuscles suffered its greatest diminution coincides pretty closely with the time when Bizzozero found the blood poorest in hæmoglobin.

From their observations on anæmic guinea-pigs and dogs, Bizzozero and Salvioli conclude that for these animals they have, in opposition to Neumann and Freyer, not only proved "the real production of colourless blood-corpuscles in the spleen, but also placed beyond doubt its true hæmatopoiétic function, and the part it takes in the formation of coloured blood-corpuscles." And they further, in support of their observations, and in opposition to those of Neumann and Freyer, bring forward the

¹ Bizzozero and Salvioli, "Ueber die Aenderungen, welche der Hämoglobingehalt des Blutes in Folge von Blutentziehungen erfährt," *Moleschott's Untersuchungen*, Bd. xii.

² Lyon, "Blutkörperzählungen bei traumatischer Anämie," *Virchow's Archiv*, Bd. lxxiv. pp. 207-247.

observations of Foa and Salvioli¹ on the embryo, which they think have placed beyond all doubt the fact that the spleen produces red blood-corpuscles in intra-uterine life.

Bizzozero was, however, not satisfied with observations on dogs and guinea-pigs, but also made researches to ascertain the function of the spleen in other animals. Having found, as already stated, that the spleens of rabbits appeared to be inactive after birth, so far as the formation of red corpuscles was concerned, he turned his attention to birds; and a paper by Bizzozero and Torre² giving the results of observations on birds is published in *Moleschott's Untersuchungen*. Their observations were chiefly on the pigeon, fowl, and finch; and they could find no indication of the formation of red blood-corpuscles in the spleens of these animals.

These conclusions are directly contrary to those which Rindfleisch³ came to, after observations on birds. Rindfleisch particularly mentioned birds as animals in which the spleen was "by far the most important producer of red blood-corpuscles."

Bizzozero and Torre found in birds, that after the production of artificial anæmia the fatty marrow became red, and actively produced red blood-corpuscles. They were able to trace all stages between the *white* corpuscles, which they believe are likewise formed in the bone-marrow, and the fully developed red corpuscles.

These observations are in accordance with those of Theo. Korn,⁴ who found that the removal of the spleen was very well borne by birds (pigeons), and did not in any way affect regeneration of the blood after the production of artificial anæmia.

Neumann considers that the experiments of Theo. Korn support the view he takes of the function of the spleen. But the error into which Neumann seems to have fallen is that, finding in rabbits that the spleen did not, at least in extra-uterine life, form red blood-corpuscles, he thence argued that the spleens of other animals, including man, were equally inactive. Bizzozero remarks, "if Neumann and Freyer had used dogs instead of rabbits, they would have come to the same conclusion as we did." This is, however, not strictly correct, as will further on be seen. For in a later paper Neumann also denies the hæmatopoïstic function of the dog's spleen.

Bizzozero and Torre⁵ also made observations on reptiles, amphibians, and fishes, the results of which were published in 1884, and are as follows:—

1. In *reptiles* and *tailless amphibians*, the *bone-marrow* forms red blood-corpuscles, which divide and multiply in it; but the *spleen* has

¹ Foa and Salvioli, "Sull' origine del globule rossi del sangue," *Archivio per le scienze mediche*, vol. iv. p. 1.

² Bizzozero and Torre, "Ueber die Entstehung und Entwicklung der rothen Blutkörperchen bei Vögeln," *Moleschott's Untersuchungen*, Bd. xii.

³ Rindfleisch, *Arch. f. mikrosk. Anat.*, Bd. xvii. pp. 21-42.

⁴ Theo. Korn, *Centralblatt f. d. med. Wiss.*, 1880, No. 41.

⁵ Bizzozero and Torre, *Virchow's Arch. f. Path. Anat. und Physiol.*, Bd. xcv Heft 1.

no function in the production of red blood-corpuscles, and is rather to be considered as a lymphatic gland.

2. In *tailed amphibians*, the *bone-marrow* appears to lose altogether its blood-forming function; and the *spleen* is the chief blood-forming organ.

3. In *fishes*, the formation and regeneration of the blood-corpuscles takes place very slowly, and occurs chiefly in the *spleen* and in blood-forming parts of the *kidney*.

Picard and Malassez,¹ from observations on dogs, came to the conclusion, that after loss of blood in spleenless animals the blood returns to its normal condition (as far as the number of corpuscles is concerned) as quickly as in animals still possessing a spleen. And they further found that extirpation of the spleen lessened the amount of hæmoglobin in the blood, but that there was an increase rather than a decrease in the number of red corpuscles.

Here again is seen the importance of distinguishing between the microcytes, which we have already considered, and the red blood-corpuscles. It seems to me that Picard and Malassez have counted the microcytes as coloured corpuscles, believing them to be young coloured corpuscles; and that it is in this way they have found an increase rather than a decrease in the number of red corpuscles.

Bizzozero attempted to ascertain the effect on the blood produced by removal of the spleen, using dogs for this purpose. He found that after spleen extirpation the hæmoglobin of the blood diminished until it reached a certain degree, and that it then began gradually to rise again. He found, however, that it never reached its former percentage while the animal remained under observation.

The experiments of Bizzozero and Salvioli to see whether after blood-letting in spleenless animals the blood returns to its original condition as quickly as in animals possessing a spleen, gave them results quite different from those of Picard and Malassez, inasmuch as they found that while the animals remained under observation the blood did not return to its former condition. They experimented on three spleenless guinea-pigs and four spleenless dogs; but say that their experiments were not extensive enough to let them come to a perfectly definite conclusion, because in the case of one dog the blood seemed to return to its previous condition as quickly as in animals possessing a spleen.

In 1869 Neumann² published a paper in which he showed that chronic diseases leading to general marasmus not only cause the red blood-forming marrow to extend itself very much, but also cause it to become very rich in nucleated red blood-corpuscles. Moreover, his observations have since received great support from those of Litten and Orth, already referred to. But, while making experiments to prove the active blood-forming function of the bone-marrow,³ he also came to the conclusion, already mentioned, that the spleen is "not a blood-

¹ Picard and Malassez, *Gazette méd. de Paris*, 1878, No. 15.

² Neumann, *Centralblatt f. d. med. Wiss.*, 1869, No. 19.

³ Neumann, *Arch. d. Heilk.*, xii. (1871), p. 187; xv. (1874), p. 470.

forming organ," at any rate "in extra-uterine life," and that even in the fœtus its action in this respect "is a very subordinate one." In fact, he grants a blood-forming action to the spleen only in a very grudging manner. He says, "in the embryo and for a short time after birth, nucleated red cells are found in the spleen; and it is possible that some of them may arise in the spleen, as there are more of them in the spleen than in the heart blood."

These conclusions of Neumann are based on his own and Freyer's researches on rabbits, already referred to; but, in the *Zeitschrift für klinische Medicin*¹ for 1881, he has, along with some observations on a case of anæmia due to prolonged and frequent loss of blood, published the results of experiments on two dogs, which he considers further to support them. He drew large quantities of blood at a time, and repeated the blood-letting six and seven times in the course of six and five-and-a-half weeks respectively. The blood drawn from the first dog in the course of six weeks amounted to one-sixth of its body-weight, and the blood drawn from the second dog in five-and-a-half weeks amounted to one-eighth of its body-weight. The second dog was reduced to a state of such profound anæmia that it died. The first dog was killed with cyanide of potassium; and the spleen was found to be very dry, and to contain "isolated nucleated coloured blood-corpuscles, which could only with difficulty be found amongst the colourless cells of the pulp." In the second dog, being the one that died of anæmia, no nucleated red corpuscles were found in the spleen. In both dogs, the red marrow had extended itself into the yellow marrow, and contained a very large number of nucleated red corpuscles.

The chief reason for objecting to the results of these experiments, as against the more numerous experiments of Bizzozero, seems to me to be the very high degree of anæmia produced. Under anæmia so great and so suddenly produced, an organ whose function had for a considerable time been laid aside or very little employed would very likely not be in sufficiently favourable circumstances for the resumption of that function. This reason, however, while applying to the spleen, would not in the same way apply to the bone-marrow. For at the very first loss of blood the bone-marrow, already in full activity, would have its activity enormously increased; although it is quite possible that its further action would be more or less paralysed by the profound state of anæmia ultimately produced.

Neumann in this paper gives the history and *post-mortem* examination of a very interesting case of anæmia from loss of blood in the human subject. The case was that of a woman, aged 38 years, who had suffered, at intervals, for three years, from great loss of blood from the uterine mucosa. She came frequently under treatment in hospital; and left improved, only to return, after some months, with similar symptoms. She died during one of the attacks; and the examination of the blood-forming organs, conducted by Neumann, yielded the following:—

¹ Neumann, "Ueber Blutregeneration und Blutbildung," *Zeitschrift für klin. Med.*, Bd. iii. Heft 3.

The *spleen* was neither enlarged nor succulent, but rather hard and dry. *Liver* was of normal size. Retro-peritoneal, mesenteric, and pelvic *glands* were distinguished by their flesh-red colour; parts being lighter, parts darker. They were not markedly swollen, and were of a hard consistence; and their cut surface was dry. The *bone-marrow* of the ribs, vertebrae, and humerus was of a dark raspberry-red colour.

Microscopic Examination.—Fatty degeneration was very widespread.

In the *bone-marrow*, from which the fat had almost disappeared, were an "astonishing number" of nucleated red blood-corpuscles. The number of these was so great that they were at least as numerous as the white corpuscles and colourless marrow-cells. There were more nucleated red corpuscles in the marrow than non-nucleated ones. "In contrast," says Neumann, "with the very distinct appearances in the bone-marrow, the results of the examination of the spleen and lymphatic glands were essentially negative."

In the *spleen*, he found nucleated red corpuscles: but so few of them that it was impossible to say that they were more numerous than in the aortic blood.

In the *lymphatic glands*, he found chiefly leucocytes, "but also, together with non-nucleated red cells, a few scattered nucleated red cells." Some of the sinuses of the glands were filled with red blood-corpuscles, having among them large blood-corpuscle-holding cells (of 0.015 to 0.02 millimetres in diameter).

This case Neumann considers very much against the blood-forming function of the spleen. But it will be noticed that *some* nucleated red corpuscles were found in the spleen, and that Neumann's explanation that they were only caught there is as yet only a conjecture. Also that under this conjecture their *absence* from the spleen of one of his dogs (the one that died of anæmia) cannot be explained.

Regarding the interesting appearances found in the *lymphatic glands*, Neumann can hardly believe that either the nucleated or the non-nucleated red corpuscles were formed there; and is much more inclined to think that they found their way into the lymph-sinuses of the glands in consequence of a diseased condition of the arterial walls. I shall refer more particularly to the lymphatic glands of this case when I speak of the blood-forming function of the lymphatic glands.

Neumann says that the *post-mortem* appearances in this case were so entirely like those of progressive pernicious anæmia that the uterus alone prevented the case from being concluded to be one of that disease. And he considers that it supports the view of idiopathic anæmia which he published in 1877,¹ viz., that that disease is due, not to a diminished production, but to an increased waste or consumption of red cells, arising from unknown causes.

In 1882–83 Dr D. G. Zesas² published two papers on the function

¹ Neumann, *Berlin. klin. Wochenschrift*, 1877, No. 47.

² Zesas, "Ueber Exstirpation der Milz am Menschen und Thiere." Zesas, "Beiträge zur Kenntniss der Blutveränderungen bei entmilzten Menschen und Thieren."—*Arch. f. klin. Chirurgie* (v. Langenbeck's), Bd. xxviii.

of the spleen. He considers that the function of the spleen is to convert white into red blood-corpuscles. He experimented on rabbits, which, it will be remembered, were the animals used by Freyer when he obtained negative results as to a blood-forming action of the spleen, and which were also the animals laid aside by Bizzozero and Salvioli, because the results obtained from them were negative. He found that four to five weeks after excision of the spleen there was a decided increase in the number of the white corpuscles in the blood, and a decrease in the number of red corpuscles. These changes increased until the tenth week, "when the blood was richest in white corpuscles, and very poor in red corpuscles." He does not give any figures; so it is impossible to say what he considers a great increase of white corpuscles, or to what extent the red corpuscles would have to be diminished before the blood could be considered "very poor in them."

In the second of those papers, as a result of an experiment on a dog from which he removed, with a lethal result, both thyroid gland and spleen at the same time, Zesas argues that after removal of the spleen alone the thyroid takes on an increased activity, and in fact replaces it; and that accordingly the removal of the spleen is borne only by an animal which still possesses a thyroid.

When I consider more particularly the supposed blood-forming function of the thyroid, I shall attempt to show how precipitate and inaccurate Zesas was in coming to any such conclusion, without first ascertaining whether an animal survived the removal of the thyroid alone.

He does not seem to have examined the blood-forming organs microscopically; and in this paper he gives the bone-marrow credit for no blood-forming function whatever. His results are in favour of the blood-forming action of the spleen, though the experiments appear to me to have been too inexact to be of very much value. In his further experiments, which I shall mention under the observations on the thyroid gland, he advances further proof of the blood-forming function of the spleen (in cats and dogs).

Having thus considered the more important views of others as to the blood-forming function of the spleen, and the experiments which seem to bear most directly on the subject, I shall now proceed to detail experiments made by myself, before attempting to draw and give my own conclusions.

My experiments, though fewer and less complete than those of some of the authors mentioned, have yet, especially when taken in connection with those of Bizzozero, enabled me to come to definite conclusions regarding the action of the spleen in the production of red blood-corpuscles during extra-uterine life. And they have further enabled me to come to definite conclusions regarding the action of the bone-marrow and lymphatic glands.

I removed the spleen from three dogs; and the method I employed for observing the effect on the blood was the enumeration of the red and white blood-corpuscles by means of Gower's "hæmocytometer." I should have liked also to estimate the percentage of hæmoglobin in the blood, but time would not permit me to do so. According, however, to the observations and opinions of Bizzozero, already quoted, the percentage of hæmoglobin in the blood has a direct relation to the number of red corpuscles; and all my observations have gone to support this view, viz., that all the red corpuscles in the circulating blood have a similar quantity of hæmoglobin, and that diminution or increase of hæmoglobin in the blood is due to diminution or increase of the number of red blood-corpuscles, and not to a smaller or greater amount of hæmoglobin in any individual corpuscles. This I know is contrary to the opinion of most physicians, and of most French authors, who believe that the hæmoglobin in the blood may be diminished even while there are a greater number of red blood-corpuscles than normal. I think, however, that this opinion has been due to including among the red corpuscles the bodies called by different writers "globules of Donné," "Körnchenbildungen," "hæmotoblasts," or "microcytes." If the view I have taken of these bodies in the first part of this paper be the correct one, the enumeration of them among the red corpuscles would quite account for a normal or increased number of red corpuscles being found along with a diminution in the percentage of hæmoglobin.

In freshly-drawn blood which is quickly examined, the red corpuscles have, to my mind, all the same colour. The hæmoglobin, however, begins to diffuse out of the corpuscles very soon after the blood is drawn, and diffuses out of some more rapidly than out of others; so that if the examination of the preparation of blood be delayed, some corpuscles will appear to be less deeply coloured by hæmoglobin than others. The effect which slight pressure or slight capillary attraction has in causing the hæmoglobin to diffuse out of the corpuscles is very marked.

In speaking, at the end of this second part of my paper, of the development of the red corpuscles, I shall give further reasons for the view of the direct relation between percentage of hæmoglobin and number of red corpuscles; and shall endeavour to show that the assumption of hæmoglobin by the corpuscles takes place under the influence of their nuclei, at the same time giving reasons for thinking that after the nucleus disappears the corpuscle has no longer the power of adding to the quantity of hæmoglobin it contains.

I kept my dogs in as good hygienic conditions as possible, in a good-sized well-lighted room. They had a full and mixed diet, and their movements in the room were little or not at all restricted.

In the excision of the spleen (and the same applies to excision of the thyroid) the animal was put under the influence of ether, which in such experiments should always be used. The animal takes the ether well, and it apparently has no bad after-effects. Antiseptic precautions were used during the operation; but as these could not have been carried out thoroughly after the operation, I did not continue them,

and used no dressing at all. I sewed up the wound with chromic-acid catgut, and latterly with horse-hair; and in every case of excision of the spleen union by first intention was obtained.

For excision of the spleen, after tying the animal out on its back and putting it under the influence of ether, I made an incision in the linea alba, immediately above the umbilicus, and about two inches long, into the abdominal cavity; and I then put my fingers (previously thoroughly washed in 1-to-20 carbolic lotion) into the left hypochondrium, where I quickly found the spleen, loosely attached to the great curvature of the stomach by the gastro-splenic omentum. I drew the spleen gently out through the wound, and secured the vessels passing to it in from four to six catgut ligatures, the tissues in which the vessels lay being included with them in the ligatures. The ligatures were then cut short, and the vessels entering the hilum were divided on the splenic side of the ligatures. The lips of the wound in the linea alba were then brought together with stitches of chromic catgut, and I was specially careful to bring the peritoneal surfaces into contact, in order that union of the peritoneal wound might at once take place, and the abdominal cavity be shut off, in case of the superficial part of the wound not healing by first intention.

The dogs all recovered very quickly from the effects of the operation. After coming out of the ether, they shivered for about a quarter of an hour; and two of them vomited once within the first half hour. But in all cases a few hours after the operation, *i.e.*, on the afternoon of the same day, the dogs were so well that no one going into the room would have supposed that they had been operated on that morning. At no time after the operation did the wound appear to give any pain. For the first day after the operation they got only milk as food; on the second day they were given also a little meat; and after that, their ordinary diet.

Before operating I always kept a dog for a week, sometimes longer, to watch whether it would lose or gain weight under its new conditions of life, and also to obtain the average number of red and white corpuscles. In the tables here given, the averages of the different estimations of the number of corpuscles before the operation are placed at the head of the corresponding columns.

The results of the examination of the blood after simple excision of the spleen were the following:¹—

Experiment I.

A female dog, with short shaggy hair, somewhat of the Scotch terrier type. About three months old, and weighing 2 kilogrammes.

¹ Compare with enumerations of the blood in normal animals given by Lyon in *Virchow's Archiv*, Bd. lxxxiv. p. 207. The slight *irregular* variations in the number of the corpuscles in my estimations were due, I believe, to the attempts the remaining blood-forming organs were making to assert themselves.

The operation was performed on 26 September 1884, and the results of the estimations of the blood may be tabulated as follows:—

	Hæmocytcs.	Leucocytes.	Proportion of Leucocytes to Hæmocytcs.
Before Operation, . . .	6,410,000	16,000	1 : 400·6
<i>Operation on 26 September.</i>			
26 September, 6 hours after, .	5,940,000	28,000	1 : 212·1
27 „ 1st day after, .	5,535,000	34,000	1 : 133·3
28 „ 2nd „ .	5,400,000	25,000	1 : 216
29 „ 3rd „ .	5,430,000	22,000	1 : 248·8
2 October, 6th „ .	5,530,000	30,000	1 : 184·3
4 „ 8th „ .	5,540,000	31,000	1 : 178·7
9 „ 13th „ .	6,000,000	24,000	1 : 250
18 „ 22nd „ .	4,900,000	23,000	1 : 213
26 „ 30th „ .	5,520,000	17,000	1 : 308·8
8 November, 43rd „ .	5,860,000	13,000	1 : 450·7
17 „ 52nd „ .	5,230,000	22,000	1 : 236·3
*25 „ 60th „ .	4,470,000	13,000	1 : 343·8
3 December, 68th „ .	5,290,000	14,000	1 : 377·8
19 „ 84th „ .	5,580,000	18,000	1 : 310
2 January, 98th „ .	6,080,000	17,000	1 : 357·6
20 „ 116th „ .	5,610,000	11,000	1 : 510
29 „ 125th „ .	6,100,000	9,000	1 : 677·7
26 February, 153rd „ .	5,730,000	11,000	1 : 520·9
13 March, 168th „ .	6,600,000	10,000	1 : 660

Experiment II.

A female dog of the English terrier type, short black-and-tan hair, ears and tail clipped short. Weight about 5 kilogrammes. At least one year, probably two years old.

	Hæmocytcs.	Leucocytes.	Proportion of Leucocytes to Hæmocytcs.
Before Operation, . . .	7,520,000	16,000	1 : 470·6
<i>Operation on 3 November.</i>			
5 November, 2nd day after, .	7,280,000	21,000	1 : 346·6
7 „ 4th „ .	7,600,000	15,000	1 : 473·3
11 „ 8th „ .	8,450,000	16,000	1 : 528·1
13 „ 10th „ .	8,610,000	8,000	1 : 1076·2
18 „ 15th „ .	8,450,000	20,000	1 : 422·5
23 „ 25th „ .	8,370,000	9,000	1 : 930
5 December, 32nd „ .	8,980,000	10,000	1 : 890
19 „ 46th „ .	8,880,000	9,000	1 : 981·1
1 January, 59th „ .	7,760,000	8,000	1 : 970
*5 „ 63rd „ .	6,590,000	17,000	1 : 387·6

Experiment III.

A female dog, probably about eight months old, but seemingly full grown; with short thick black-and-white hair. Weight slightly over 5 kilogrammes.

	Hæmocytæ.	Leucocytes.	Proportion of Leucocytes to Hæmocytæ.
Before Operation, . . .	7,000,000	6,000	1 : 1168·2
<i>Operation on 15 November.</i>			
19 November, 4th day after, .	6,700,000	16,000	1 : 418·7
23 " 8th " . . .	7,220,000	12,000	1 : 601·6
27 " 12th " . . .	7,600,000	8,000	1 : 937·5
2 December, 17th " . . .	6,850,000	6,000	1 : 1141·6
9 " 24th " . . .	6,130,000	22,000	1 : 276·6
22 " 37th " . . .	5,800,000	8,000	1 : 725
3 January, 49th " . . .	5,270,000	18,000	1 : 292·7
14 " 60th " . . .	5,720,000	12,000	1 : 478·5
27 " 73rd " . . .	5,770,000	10,000	1 : 577
*13 February, 90th " . . .	4,810,000	10,000	1 : 481
2 March, 107th " . . .	6,050,000	7,000	1 : 864
8 " 108th " . . .	6,590,000	6,000	1 : 1098

In the dog of *Experiment I.*, the changes seem to have occurred quickly, chiefly within the first two months. They consisted in a decrease of the number of red corpuscles and a relative and absolute increase in the number of white corpuscles in the blood. The greatest decrease in the number of red corpuscles, as will be seen from the tables,¹ was found two months after the operation. After reaching a minimum, the red corpuscles then increased again in numbers, though not very regularly; and the relation of the white corpuscles to the red gradually approached that which had existed before the operation.

The increase in the number of white corpuscles, though it corresponded to a certain extent with the decrease in the number of red, did not correspond very regularly. The great increase for the first day or two was due, in part at least, to the operation. For the white corpuscles always rise in number, and the red corpuscles always fall in number, for a day or two after an operation; and that without any regular proportion to the amount of blood lost. Such changes due to an operation are always recovered from in about two days.

¹ Marked by *.

On the 13th of March, the day of the last estimation, and five-and-a-half months after the operation, the red corpuscles were slightly more than their original number. The fact, too, that the white corpuscles had then sunk below their original number seems to me to be likewise of significance, as indicating that the gland removed had for one of its functions the production of white blood-corpuscles. The important result of the blood estimations, however, is the distinct change observed in the number of *red* blood-corpuscles. From this change it would appear that [the gland, if not taking a *great* part, must at any rate have taken *some* part in the formation of the red blood-corpuscles; and that although the other blood-forming organs had increased their activity, they had yet failed to bring the red corpuscles up to their normal number again until nearly six months after the operation.

That the removal of the spleen had little or no effect on the growth of the animal, will be pretty evident when I state that the weight of the animal was 2 kilogrammes before the operation; that it began to gain in weight almost immediately after the operation, and to increase in size; and that its weight on the 26th of February (five months after the operation) was 4 kilogrammes and 34 decagrammes. The dog was then in as good condition as on the day of operation, and, as will be seen, had doubled its weight (owing to increase in size). From the day of the operation to the day of its death, it was the picture of a healthy animal; and certainly there was not the slightest sign interference with digestion, which would be expected if Schiff's¹ view of the relation of the spleen to pancreatic digestion were admitted. It took its food even more greedily after the operation than previously. In fact the behaviour of my dogs would rather support the statement that after the removal of the spleen the appetite is increased.

In *Experiment II.*, the results obtained were at first sight a little confusing: still they may, I think, be taken as likewise in favour of a blood-forming action of the spleen. It will be noticed that there was a distinct fall in the number of corpuscles in the blood two months after the operation: the confusing point is that just after an initial slight fall, and apparently as the

¹ Schiff, *Schweizer. Zeitschrift f. Heilkunde*, Bd. i. (1862).

immediate result of the extirpation, there was an increase rather than a decrease in the number of red corpuscles. Taking all the facts together, I think the results obtained from the experiment (in which the animal, it will be remembered, was about two years old) still support the blood-forming function of the spleen, but point to that function being in adult life almost in abeyance. I think they show that even in adult life the spleen has some activity; and it seems to me that even the increase in the number of red blood-corpuscles after the operation, instead of being against this view, is rather in favour of it. For the increase might be explained by considering the spleen as a blood-forming organ, and supposing that on its removal the other blood-forming organs, which had previously been doing most of the work, were thereby stimulated to a greater activity that more than compensated for its absence. The explanation of the subsequent fall might be either that the bone-marrow and other blood-forming organs had been unable to maintain this high state of activity, or that the fall was merely part of an oscillation about the normal point.

It will be noticed that the white corpuscles were diminished in number both relatively and absolutely, and that afterwards there was a slight increase in their number, concomitant with the decrease in the number of red corpuscles.

An interesting point with regard to the animal is that it had an unusually well developed thyroid gland, which, however, did not enlarge after removal of the spleen. I shall subsequently consider the question of this dog's thyroid under the effects of excision of the thyroid, in the third part of this paper.

In *Experiment III.*, where a positive result was again obtained, we were dealing with a dog within the first year of extra-uterine life, though having already the appearance of being full-grown.

In the case of this animal, the number of red corpuscles gradually decreased for the first six or seven weeks; next there was a hardly perceptible rise; and then they sank to their lowest point, reaching it three months after the excision. The white corpuscles increased both absolutely and relatively in number, though not in a very regular manner. Towards the middle of the fourth month they had begun to sink in number,

and if the dog had been allowed to live longer they would probably have sunk even below their original number. The diminution of the red corpuscles in this dog was really a decided one, amounting to quite 2,000,000 out of every 7,000,000.

The time of the greatest diminution of the red corpuscles corresponds pretty well in all three dogs, being between eight and twelve weeks; and it also corresponds with the time given by Zesas (ten weeks), as well as, interestingly enough, with the time given by Credé (two months).

The last dog, like both the others, recovered very quickly after the operation; took its food very well; and after losing weight for the first day or two, increased again until it reached its former weight, at which it remained, weighing on the 3rd of March exactly the same as on the day of operation. Here also there were no signs of interference with digestion, and the dog would have been taken by any one for a perfectly healthy animal.

During the examination of the blood of the dogs, I was never able to convince myself of the presence of any nucleated red corpuscles in it.

Post-mortem Appearances.—Of the three dogs from which I excised the spleen, only one was allowed to live without further operation, viz., the dog of Experiment I. In the dog of Experiment III. I afterwards produced artificial anæmia, in order to see the condition of the blood-forming organs in a spleenless animal during the process of blood-regeneration. The dog of Experiment II. was used also for excision of the thyroid, and its further history will be given under the head of that gland.

The dog of *Experiment I.* (on which no further operation was performed), on being killed after the expiry of five-and-a-half months, showed the following appearances:—

Body well nourished; neither more nor less fat than usual. No naked-eye abnormal appearances, with the exception of the absence of the spleen. There was not the least sign of there having been any irritation in the abdomen, either in the region from which the spleen had been removed or elsewhere. The liver, which has been noticed by Zesas to be larger in animals after removal of the spleen, was not distinctly enlarged, nor more than usually rich in blood.

The tissues to which I paid particular attention were the bone-marrow, the lymphatic glands, and the thyroid gland. In the bone-marrow and lymphatic glands I found evidence of blood-formation, but not in the thyroid gland.

As to the *bone-marrow*, I found evidence of blood-formation

chiefly in the *red* marrow of the ribs, the vertebral bodies, and the heads of the long bones; in short, in marrow of spongy bone. But I also found that the usually fatty marrow of the shafts of the humerus and femur had to some extent been transformed into red marrow, *i.e.*, was much redder than fatty marrow, though not so red as red marrow, and, further, presented microscopic appearances intermediate between red and yellow marrow. This change of the fatty marrow supports in an interesting way the blood-forming function of the spleen, especially if compared with the observations of Litten and Orth already referred to.—The marrow in the shafts of the other long bones had remained fatty.

The marrow was examined fresh, and either undiluted or diluted with a neutral fluid. I preferred the latter method; because the only semi-fluid marrow could not be satisfactorily examined without dilution. For diluting fluid, a solution of sulphate of soda, of sp. gr. 1.022, was used; and as it was difficult to get an idea of the number of nucleated red cells in the marrow when the nuclei were uncoloured, the faintest trace of methyl-violet was added to the solution. It is impossible to say how much methyl-violet should be used: the amount needed is so small. It is best to use enough, but no more than enough, to colour the nuclei of the red and white cells. The addition of such a trace of methyl-violet to the "artificial serum" appears also to have the advantage of rendering it even less liable to alter the shape of the red corpuscles. This has been remarked by various observers.

For the examination of the marrow, I first placed a drop of the diluting solution on a slide; then mixed the marrow with the drop, at the same time to some extent teasing it out; and, lastly, put on a cover-glass, pressing it gently down on the preparation so as to leave only a single layer of cells. In the case of spongy bone, I squeezed out the marrow by means of a pair of bone-forceps, and so obtained a semi-fluid marrow free from bony spicules.

The red marrow of a normal dog, when thus treated, with or without staining, shows numerous nucleated colourless cells of different sizes, varying from about 8 *micros.* to as much as 16 *micros.* in diameter. The nuclei are almost always relatively

large; and they are more or less coarsely granular, this being due partly at least to an intranuclear net-work. The perinuclear protoplasm is faintly granular. Among the cells there are always a very considerable number of ordinary red blood-corpuscles. In addition, however, there are cells which can be distinctly recognised as nucleated red blood-corpuscles. These cells, as has already been said, are best seen when a trace of methyl-violet is added to the artificial serum in which they are examined. The methyl-violet has the effect of staining their nuclei, as well as the nuclei of the colourless cells of the marrow, and also of staining to a slight extent the perinuclear protoplasm of the colourless cells. Various stages may be seen in the development of the nucleated red cells in the bone-marrow, but the stage which is most characteristic, and which it would be difficult to mistake for anything but a nucleated red blood-corpuscle, is that where the cell is rather larger than a non-nucleated red blood-corpuscle, and has a nucleus which is not large as compared with the cell, and perinuclear substance which is as darkly hæmoglobin-tinted as a non-nucleated red corpuscle (fig. 1, *d*).¹ Of this variety of cell, only a few can be seen in the red marrow of a normal dog. But there are numbers of what I consider to be earlier stages in the development of these cells from the ordinary cells of the marrow (fig. 1, *b* and *c*). Many of them, especially those of from 10 to 12 or even 14 *micros.* in diameter, have a relatively very large nucleus with a very well defined outline (fig. 1, *a*). Filling up the interval between the nucleus and the capsule of some of these cells can be seen a thin yellow band, which I take to be the first appearance of hæmoglobin in them (fig. 1, *b*). So thin is the earliest yellow band, that it could be taken as significant of nothing, were it not for the fact that what must be later conditions of such cells can be seen, where it has become broader (fig. 1, *c*). And, indeed, all stages of transition can be seen, between the large cells, with their large nuclei and very thin band of hæmoglobin-coloured perinuclear substance, and the typical nucleated red corpuscle, which is much smaller, and has a much smaller nucleus and a broad coloured band. As a rule, the band of hæmoglobin-coloured substance occupies the whole space

¹ The figure will be given in the next number of the *Journal*.

between the cell-envelope and the nucleus; but occasionally there can be seen a small amount of colourless substance immediately surrounding the nucleus, and still taking on the methyl-violet colouring. I have seen this remnant of the perinuclear finely granular substance of the cell only in the younger stages of development, never in a typical nucleated red cell.

To return to the *post-mortem* appearances of the dog (*Expt. I.*):—

The *bone-marrow* of the ribs, squeezed out, as stated, and mixed with the methyl-violet-tinted sodium-sulphate solution, showed great numbers of very young nucleated red cells; and here and there could be found nucleated red cells of the more typical variety. Nucleated red cells crenate very easily, thus giving an additional proof of their relation to the non-nucleated red cells.

The marrow from the heads of the femur and humerus showed enormous numbers of nucleated cells in the early stage of development: a greater number even than was found in the ribs. Also a few of the more typical variety.

The partially reddened marrow of the shafts of the humerus and femur contained a few examples of developing red cells.

In the *lymphatic glands*, very interesting and unexpected appearances were found. The glands of the mesentery were distinctly enlarged, when compared with those of normal dogs; and they were distinctly succulent, though not decidedly redder than usual. A scraping from the cut surface of these glands, mixed with the methyl-violet-tinted sodium-sulphate solution, showed numbers of nucleated red cells, in earlier and later stages of development. There could be no doubt about them: for there were a few in every field; and quite as many of the later stages could be found as in the marrow of the ribs. This observation will be more interesting when it is compared with what I shall afterwards describe as having been found by me in the lymphatic glands of an animal whose thoracic duct I had tied some time previously.

The *thyroid gland*, when similarly examined, showed no signs of a blood-forming function.

I now pass to the dog on which *Experiment III.* was performed, and which I subsequently bled for the purpose of producing artificial anæmia. On referring back, we see that on the 3rd of March, nearly four months after the operation of excision of the spleen, this animal had a number of red corpuscles per cubic millimeter of blood almost as great as the original number, and that the white corpuscles had almost their original relation to the red.

Experiment IV.

Dog previously used for Experiment III.

On the 3rd of March I drew from the left carotid 20 c.c. of blood, being scarcely $\frac{1}{2}$ per cent. of the body-weight; and on the following days I estimated the blood, to notice the effect. In cases of drawing blood, as well as in my other experiments, I always put the animal under the influence of ether.

	Hæmocytcs.	Leucocytes.	Proportion of Leucocytes to Hæmocytcs.
Before Operation, . . .	6,590,000	6,000	1 : 1098·3
<i>Operation on 3 March.</i>			
4 March, 1st day after, . .	5,690,000	13,000	1 : 437·6
5 „ 2nd „ . .	6,060,000	10,000	1 : 606
6 „ 3rd „ . .	6,250,000	8,000	1 : 781·2
9 „ 6th „ . .	6,270,000	5,000	1 : 1254

Six days after the loss of blood, which must be taken as an extremely small one, the corpuscles had not quite returned to their previous numbers; showing that blood-formation was not so rapid as usual.¹

As a proof, however, that in spleenless animals the blood is not so rapidly regenerated, the experiment cannot alone be considered of much value.

On the 9th of March, I drew from the same carotid artery (the previous wound having in the meantime healed) a considerably larger quantity of blood, viz., 75 c.c., being about 1·8 per cent. of the body-weight.

The dog recovered quickly from the operation, and was well next day, though not so lively as usual, being more inclined to sleep, and

¹ Compare with results of Lyon's experiments, *Virchow's Archiv*, Bd. lxxxiv.

less active in its movements. The amount of anæmia produced will be evident from the following table :—

	Hæmocytcs.	Leucocytes.	Proportion of Leucocytes to Hæmocytcs.
Before Operation, . . .	6,270,000	5,000	1 : 1254
<i>Operation on 9 March.</i>			
11 March, 2nd day after, . .	4,400,000	7,000	1 : 628·5
14 „ 5th „ . .	4,490,000	9,000	1 : 498·3

The loss of blood had produced a very considerable degree of anæmia; and in this instance sufficient time did not elapse before I killed the animal to enable me to see to what extent the remaining blood-forming organs would be able to regenerate the blood, and how long it would take them to do so.

Post-mortem appearances, after killing with ether, on the 14th of March :—

Bone-marrow.—The marrow of the ribs contained a great many nucleated red cells, some of which had very small nuclei (fig. 1, *e*).

The marrow in the whole length of the shafts of the humerus and femur was red, and contained great numbers of the early stages of nucleated red cells, as well as a fair number of the more typical nucleated red cells.

The marrow in the heads of the long bones and the marrow of the bodies of the vertebræ contained a greater number of developing red cells than the marrow in the shafts of the long bones, but not so many as the marrow of the ribs. Most of the cells were in the earlier stages.

The comparative rarity of the later stages of the developing red corpuscles, except in the marrow of the ribs, and the great numbers of the earlier stages, correspond entirely with the blood enumerations. For according to these the regeneration of the blood had even on the day of death hardly yet begun.

Lymphatic Glands.—Those of the abdomen were large and rather succulent, and if anything somewhat redder in the centre than usual. Some nucleated red cells were found, but not very many. There were, however, a considerable number of white cells with peculiarly clear perinuclear substance, which looked

as if they needed nothing but hæmoglobin to convert them into nucleated red cells.

Thyroid Gland.—Of usual size, most unusually pale, and presenting no appearance of a blood-forming function.

In the abdomen there were not the faintest appearances of any irritation having followed the removal of the spleen.

Up to this time I have been dealing with animals from which I had excised the spleen; and I think that my experiments furnish pretty conclusive proof that the spleen has in *ordinary conditions* a blood-forming action, if perhaps a subordinate one, throughout extra-uterine life, its activity being, however, probably greater during the first year of life. The facts in favour of this action are:—

1. The changes in the blood, consisting in a primary decrease in the number of red corpuscles and increase in the number of white, and in one case (Expt. I.) a secondary decrease of the white corpuscles below their original number after the red corpuscles had already returned to their original number. The secondary decrease in the number of white corpuscles, which corresponds with the observations on the blood of Credé's patient three years after the extirpation of the spleen, points to the probable reason for the primary increase, viz., that an organ had been removed having, on the one hand, the function of transforming white corpuscles into red, and on the other hand the function of itself producing white corpuscles.

2. The partial transformation of the yellow marrow of the shafts of the humerus and femur into red marrow.

3. The appearance of a considerable number of nucleated red cells in the lymphatic glands, only very few nucleated red cells being found in the lymphatic glands under ordinary conditions.

I next tried to ascertain the truth of Bizzozero's assertion that the spleen is brought into fresh activity by the production of artificial anæmia. Experiment IV., already described, had given some evidence of a negative character in favour of Bizzozero's view: for in it, after blood-letting in the spleenless animal, the regeneration of the blood did not take place as rapidly as, according to Lyon, it would in animals possessing spleens have done. The *post-mortem* appearances were similar to those found in the dog of Experiment I., being merely somewhat exaggerated,

owing to the efforts of the remaining organs to overcome the artificial anæmia which had been produced.

I was only able to perform one experiment for the purpose of ascertaining whether I could get any positive evidence in favour of Bizzozero's conclusion, but from it fortunately got very decided evidence of the kind.

Experiment V.

A very healthy female dog, about two years old, a mixture of pug and terrier. Weight 6 kilogrammes 20 decagrammes.

On the 10th of March I drew from the right carotid 140 cubic centimetres of blood, being about 2·6 per cent. of the body-weight. Then I left the animal for three days, feeding it as usual, and finding that during this time it did not lose weight. And then I killed it with ether, and examined the blood-forming organs.

Spleen.—Unusually large, soft, and succulent, and of the rose-red colour which Bizzozero describes as so characteristic of a spleen containing many nucleated red cells.

A scraping, examined in the usual way, showed very numerous nucleated red cells, many of which were in process of division. Many of the cells were in the earlier stages of nucleated red cells, but there were also a very large number in the later and more typical stages. There could be no doubt about these cells having been formed here. For their number, although smaller than the number found in the marrow of the ribs, was yet far above what could be accounted for by the supposition of nucleated red cells having been entangled in the spleen from the circulating blood. Moreover, the occurrence of the red cells in their different stages of development and the occurrence of the dividing red cells are very much against any such supposition.

Lymphatic Glands.—Were perhaps a little larger than usual, but were no redder. A scraping from the the cut surface of a mesenteric gland showed many nucleated red cells, with very faintly coloured perinuclear substance, as well as a fair number of non-nucleated red cells. The bronchial glands showed the same appearances.

Bone-Marrow.—The marrow of the ribs was of a very rich brown colour. In it were found enormous numbers of nucleated red cells, in all stages of development. These cells were more deeply hæmoglobin-tinted than those found in the lymph glands,

but were otherwise the same cells. The shafts of the femur and humerus were filled with a very rich red marrow, which contained numerous nucleated red cells, though not so many as the marrow in the heads of the bones. The marrow in the heads of the bones contained fewer than that of the ribs.

There was a complication in this experiment, inasmuch as I had previously (three weeks before the blood-letting) removed from the animal one lobe of the thyroid gland. The case might therefore be interpreted as supporting the views of those who believe that the spleen and thyroid have a mutual compensatory function; and unfortunately I cannot altogether deny that such an interpretation is possible. But all my observations on the thyroid are greatly against its having a function similar to that of the spleen. I have, in fact, found no evidence of its having any blood-forming function. The dog in this experiment had suffered in no way from the removal of one lobe; and I shall further on, under the head of the thyroid gland, give other cases, both in animals and in the human subject, where removal of one lobe had no effect whatever. The examination of the remaining lobe of the *thyroid gland*, which was *not* distinctly enlarged, revealed no signs of a blood-forming function.

I next, in order to be able to look at the question from as many sides as possible, estimated in two animals the numbers of red and white corpuscles in the splenic artery and vein, to see whether Bizzozero's observations on this point could be confirmed. It will be remembered that he found, or concluded that he found, an increase in the number of red corpuscles, and a relatively still greater increase in the number of white corpuscles, in the splenic vein, over the numbers in the splenic artery.

The results of my two observations were not very marked, but they pointed in the same direction as the results of Bizzozero's experiments.

Experiment VI.

The first enumeration was taken from the blood of the splenic artery and splenic vein of a dog whose thoracic duct I had tied some time previously (with a result to be afterwards described).

When about to kill the animal, I put it under ether, and cut directly down upon the spleen, on the outer border of the left rectus

abdominis, just below the ribs. A good free incision was made, so that I could draw the spleen out of the abdomen without in any way squeezing it, and without drawing on its blood-vessels. After clearing its vessels as carefully as possible, I made with a needle a puncture in the splenic vein sufficiently large to let the blood flow very freely. I made the puncture in the vein first, because a permanent wound in the vein would not affect the number of corpuscles in the blood of the artery, while if I had first taken blood from the artery and had happened to stop the flow in it, I should probably have found little or no blood in the vein when it was opened. After the required quantity of blood had been got from the vein, the gentlest pressure of a sponge for a minute sufficed to stop the flow from the wound in its walls; and this seemed to have become closed, as the circulation went on as before. I then made a puncture in the artery, and took the required quantity of blood while it came freely spurting out. The enumeration of the red and white corpuscles gave the following:—

Splenic Vein.

Hæmocytes 9,600,000. Leucocytes 11,000. Relative number of Leucocytes to Hæmocytes 1 : 872·7.

Splenic Artery.

Hæmocytes 9,410,000. Leucocytes 9,000. Relative number of Leucocytes to Hæmocytes 1 : 1045·5.

These figures support the results of Bizzozero, though not in a very pronounced manner, especially as the spleen in this experiment contained (as will later more particularly be stated) a moderate number of developing red blood-corpuscles, and was therefore more active than the spleen of a normal animal. And here, indeed, it must be remembered that Bizzozero's own observations, made as they were on animals which had been rendered anæmic, were likewise made under conditions in which the spleen was actively producing red blood-corpuscles.

We cannot expect that a very decided number of fresh red corpuscles should be added to every cubic millimeter of blood which passes through the spleen; and we must, I think, be content to allow that if the blood of the splenic vein contains at all a greater number of red corpuscles than the blood of the artery, then the spleen has really a blood-forming function.

Moreover, the function of the spleen as a producer of white corpuscles is likewise supported, if indeed it needed any other than a histological support.

I found no nucleated red corpuscles in the blood of either vein or artery.

Experiment VII.

The second dog from which I got such an enumeration was the one I made artificially anæmic (Experiment V.) to see if the activity of the spleen would be increased. The steps taken for the enumeration were the same as in Experiment VI. The results, although in favour of the same conclusion as those of that experiment, were still less decided. This is remarkable, as the spleen was very rich in developing red cells.

Splenic Vein.

Hæmocytes 6,310,000. Leucocytes 9,000. Relative number of Leucocytes to Hæmocytes 1 : 701·1.

Splenic Artery.

Hæmocytes 6,250,000. Leucocytes 8,000. Relative number of Leucocytes to Hæmocytes 1 : 781·2.

These slight differences between the numbers of corpuscles in the vein and artery are quite in accordance with the observations of those writers who could find no difference between the contents of the vein and the contents of the artery in normal conditions. For if the difference is so slight when the spleen is actively forming red cells, it must be still slighter when the spleen is comparatively inactive. In other words, the addition of red corpuscles to a cubic millimetre of blood in passing through the spleen must in normal conditions be so small as to make it practically impossible to observe any numerical difference between the corpuscles in the artery and the corpuscles in the vein.

But here another point must not be lost sight of, viz., what is stated by many authors to be one of the functions of the spleen, the breaking down of red blood-corpuscles. Later in my paper I shall speak of reasons for supporting this as one of the functions of the spleen. If the spleen possesses any such function, the increase in the number of red corpuscles in the splenic vein over the number in the splenic artery would be no index of the number of fresh corpuscles added to the blood in its passage through the spleen.

(To be continued in the next number.)

Anatomical Notices.

MALFORMATIONS OF PELVIS AND PELVIC ORGANS IN A FŒTUS. By JOHN PALMER, L.R.C.P. Lond., M.R.C.S. Eng.

Mrs J. was delivered of twins on the 1st of June 1884 (a month earlier than she expected). The first child was a girl, living and looking like a fœtus of between 7 and 8 months, the second child was small and looked like a fœtus at about the 6th month, this child lived five hours; the first child is living now and is a very fine girl, the mother says as large as any of her children have been at the same age (14 months).

On superficial examination of the second child, the pelvis was found to be extremely small, and no external opening could be found; in the middle line, a little below the lower end of sacrum, was a very small projection of skin with a small depression extending round it; farther forward, a little below the symphysis pubis in the middle line, was a small nipple-like projection of skin, but no opening in or around it; the appearance is represented in fig. 1.

On *post-mortem* examination of chest, heart and lungs were found to be normal; and on opening abdomen, liver, spleen, suprarenal bodies, small and large intestines as far as sigmoid flexure were normal, cæcum in right iliac fossa; in left iliac fossa the descending colon ended in a large closed dilatation measuring in length 2 inches, in width $1\frac{1}{2}$ inches; no trace of rectum either as a fibrous cord or otherwise could be found. The cavity of pelvis, which was very shallow and small, measured transversely $\frac{3}{4}$ of an inch, antero-posteriorly $\frac{5}{16}$ of an inch; in it was the lower part of a closed sac which measured in length from above downward $1\frac{1}{2}$ inches and transversely $1\frac{1}{2}$ inches. This sac on being opened was found to contain about two teaspoonfuls of milky-looking fluid, which under the microscope showed epithelial and fat cells and debris, the pouch at end of descending colon was attached to the upper and left side of this by connective tissue (their cavities did not communicate). Into the sides of this closed sac at its upper part were seen to be inserted two thickened cords which suddenly became fine tubes (Fallopian tubes), and were contained in the broad ligaments, the ovaries lying immediately below the fine tubes, the thickened portions apparently represented the two halves

of an undeveloped uterus; the round ligaments were large, normal in position and destination. Reaching rather higher up than this sac, and somewhat to the left side, and extending downward behind to its base, being closely adherent to its posterior wall, was another sac, oblong in shape, the upper extremity pointed and continued into a tube which passed upward and was attached to the left kidney, higher than the hilus; this sac, on being opened, was found to contain clear urine, the walls of the sac were thin, into its base the right and left ureters entered. These two sacs, which represented the vagina and bladder, were almost entirely situated in the false pelvis and lower part of abdomen, the bladder being quite posterior. The left kidney measured $1\frac{3}{4}$ inches in length and $\frac{7}{10}$ of an inch across, was wholly composed of cysts, and from it two tubes passed to the bladder, one the ureter, which was attached at the hilus, the other, attached above the hilus and ending in the apex of bladder as before mentioned. The right kidney was very small, also cystic; it measured $\frac{4}{10}$ of an inch in length and $\frac{1}{4}$ of an inch in width; the kidneys were in the normal positions, except that the right ureter being short, the corresponding kidney was somewhat lower down than usual. Fig. 2 shows the relative positions of the internal parts.

On examining the pelvis the symphysis pubis was found continued downward and backward to the posterior part of the tubera ischia; the rami of ischia and pubes being close together and held in apposition by fibrous tissue, so that there was slight mobility; the only outlet to pelvis was behind this and in front of sacrum, a space only large enough to admit the tip of the little finger; the two internal obturator muscles covered the cartilages and formed the floor of pelvis. At the umbilicus only one hypogastric artery was found and no urachus.

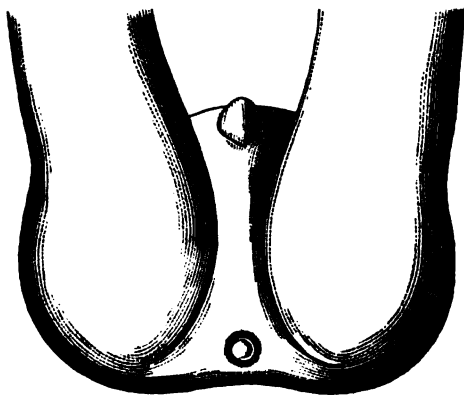


Fig. 1.

FIG. 1.—The external appearance of perinæum of fœtus, legs acutely flexed on the abdomen.

FIG. 2.—The relative position of genito-urinary organs; R.K., L.K., right and left kidney; B., bladder ending above in a fine tube attached to upper part of left kidney; V., closed vaginal sac; B.L., B.L., broad

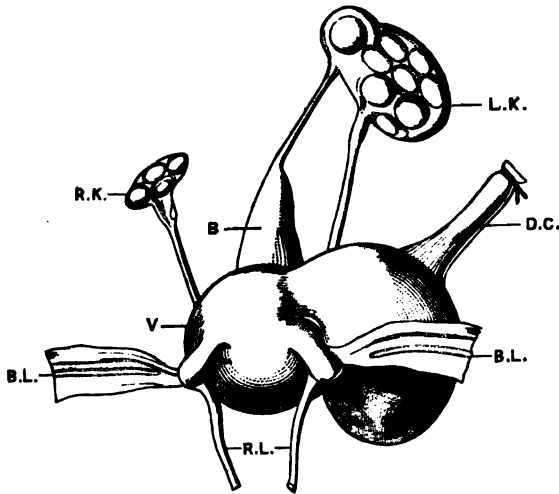


Fig. 2.

ligaments with halves of uterus internally and Fallopian tubes and ovaries in outer part; D.C., descending colon ending in large closed pouch; R.L., round ligaments of uterus.

ON AN ANOMALOUS MUSCLE IN THE FRONT OF THE
NECK IN A HUMAN SUBJECT—A STERNO-PETROSO-
PHARYNGEUS. By G. E. RENNIE, B.A. (Sydney), *Student
of Medicine, University College, London.*

THIS peculiar muscle was met with in the course of a dissection of the anterior triangle of the neck, in a well-developed muscular male subject, which was brought into the dissecting room of University College, London, during the month of October 1884; and acting upon the suggestion of Professor Thane, I have prepared the following account of it for publication:—

The muscle took its origin from the anterior surface of the manubrium, immediately internal to the sternal head of the right sterno-mastoid, by a thin flat tendon, nearly half an inch wide, and about half an inch long, extending higher on the posterior than on the anterior aspect of the muscle. The tendon gave rise to muscular fibres which formed a somewhat rounded bundle, some two or three lines in diameter. The muscle then passed up the right side of the neck, superficial to the sterno-hyoid, sterno-thyroid, and omo-hyoid muscles, then over the hypoglossal nerve, and then passing between the internal and external carotid arteries, disappeared beneath the digastric and stylo-hyoid muscles. On being traced subsequently to its termination, the muscle was seen to split up, at about two inches from its insertion, into three sets of fibres, the disposition of which was as follows:—(1) One set of fibres passed directly upwards, and was inserted into the vaginal process of the temporal bone, the inner fibres of insertion being in immediate contact with those of origin of the levator palati. (2) Another smaller set, turned slightly inwards, and passing beneath the lower border of the superior constrictor, blended with the pharyngeal aponeurosis, under cover of that muscle. (3) A third set, much shorter than the preceding, turned a little outward and forward, and blended with the lower fibres of the superior constrictor muscle of the pharynx.

The muscle was completely surrounded by the deep cervical fascia, as that structure passed forwards from the anterior border of the sterno-mastoid, and had the following relations to surrounding structures:—

(a) *To Muscles*.—It rested upon the sterno-hyoid, sterno-thyroid, and anterior belly of omo-hyoid; then upon the middle constrictor of the pharynx. It was crossed by the posterior belly of the digastric and the stylo-hyoid, and higher up by the stylo-pharyngeus; and in this case by an accessory slip from that muscle to the great cornu of the hyoid bone. To its outer border, for about half its length, and at a distance of half an inch from it, was the sterno-mastoid.

(b) *To Vessels*.—It was crossed superficially at its lower part by the anterior jugular vein, and higher up by a communicating branch between the external and anterior jugular veins. It passed over the facial vein, and then sinking inwards between the two carotid arteries, lay to the inner side of the external carotid. A small vein from the substance of the muscle entered the internal jugular vein.

(c) *To Nerves*.—It was supplied by a small twig from the glossopharyngeal nerve which entered it on its outer surface. The muscle in its upward course crossed over the branch of the descendens noni to the anterior belly of the omo-hyoid, the hypoglossal, and the glossopharyngeal nerves.

I have not been able to find any account of a similar muscle on record. Macalister, in *Transactions of Royal Irish Academy*, 1871, refers to one case in which a slip from the anterior margin of the sterno-mastoid was inserted into the tympanic ring; and this is the only record I can find of an insertion of any part of the

sterno-mastoid into the petrous part of the temporal. I have also consulted Testut's *Anomalie Musculaire*, Gruber's *Anatomische Notizen* in *Virchow's Archiv*, and also Meckel's *Vergleichende Anatomie*, but have failed to gain from them any information bearing upon this peculiar abnormality.

In conclusion, I have to acknowledge my indebtedness to Professor Thane for kindly advice, and for lending me works of reference.

NOTE ON A CASE OF CONGENITAL HYPERTROPHY OF
THE LEG. (Diffuse Venous Nævus.) By GILBERT
BARLING, M.B.

THE specimen which I had the opportunity of dissecting was the left leg of a man, aged fifty years, who stated that at his birth the left leg was larger round than the right, and that the left foot was deformed, but, except for the weight of the limb, he had not suffered much inconvenience, and had until recently been able to get about quite actively.

I had no opportunity of making comparative measurements of the two legs, but, roughly speaking, the left leg, from a little above the knee downwards, was about three times the size of the right. The enlargement was not quite uniform, affecting chiefly the posterior surface, and not extending further on the foot than the base of the metatarsus. There was varicosity of the smaller skin veins, but there was no ulceration of the skin, nor had there been any. To the feel, the soft tissues of the leg gave the sensation of a lipoma with many dense fibrous septa. The foot was in a condition of calcareo-valgus. When the skin was removed, the subcutaneous tissue was found greatly thickened, partly from an increase of fat, but mainly from an abundance of fibrous tissue, in which were imbedded a large number of small, thin-walled and tortuous veins; from this thick layer, septa passed to the deep parts of the leg, ensheathing the muscles, &c. The posterior muscles appeared to have retained their shape and size, but the muscular fibres were almost replaced by fat, without, however, any nævus condition. The tendo Achillis and its sheath were so blended with the surrounding fatty and fibrous tissues as to be indistinguishable from them, but the other posterior tendons and their sheaths were healthy, except that the sheaths were thickened by the nævus tissue.

The anterior muscles, though small, appeared to have healthy fibres, but all of them, except the tibialis anticus, were shortened, and their sheaths were generally thickened with nævus tissue.

The peroneus, longus, and brevis, though of good size, had undergone fatty change to a considerable extent, and they were shortened.

On division of the tendons of the extensor longus digitorum, the extensor proprius pollicis, and all three peronei, the foot was easily brought down to a right angle with the leg, but there still remained a considerable amount of outward rotation of the anterior part of the foot at the transverse tarsal joint.

The posterior tibial vein was single and much enlarged, so much so as to admit of one's little finger being passed into it.

The principal nerves were all thickened, but the posterior tibial was especially so, its circumference being quite as great as that of an ordinary sciatic. Microscopically, this enlargement was seen to be due to an increase of the epineurium and perineurium.

The bones of the leg were fairly developed as regards size, but they were deficient in weight, and their surfaces presented numerous irregular outgrowths, such as are sometimes seen at the insertion of tendons in the lower extremity, though here quite independent of those attachments.

The bones of the foot were in marked contrast to those of the leg, being small, feeble, and much distorted, the deformity falling chiefly upon the os calcis, which was hardly recognisable, as it was mostly represented by a thin vertical plate supporting a small horizontal plate projecting from its side.

NOTE ON THE MANDIBULAR DENTITION OF THE SHREWS. By G. E. Dobson, M.A., F.R.S.

THE Shrews (*Soricidae*) form a very compact family of Insectivora, the species of which, among other points of close resemblance one to another, are believed to possess the remarkable peculiarity of having, whatever may be the number of the upper teeth, invariably six pairs of mandibular teeth, of which the first on each side is considered an incisor, the second a canine, the third a premolar, and the remaining three molars. It was, therefore, with much interest that I lately discovered a rudimentary seventh pair of mandibular teeth in the otherwise also remarkable species *Myosorex varius*, Smuts., of South Africa. The very small additional tooth exists (in every specimen examined) on each side between the second and third teeth; it is quite invisible to the naked eye, but may be readily made out, by the aid of an ordinary lens lying between the upper surface of the hinder part of the base of the second tooth and the under surface of the overlapping fore part of the base of the third tooth, which leave its small extremity alone uncovered. The direction of the cusp of this tooth is such that,

if produced, it would come in front of the first maxillary tooth, and therefore should, according to the system of dental notation now in use, be considered the lower canine, whence it would naturally appear to follow that no lower canine exists in any other species of the family. This and other interesting questions connected with the dentition of the Shrews I hope to deal with fully in Part III. of my Monograph of the Insectivora, which will be ready for publication in a few months.

Fig. 1.



Fig. 2.

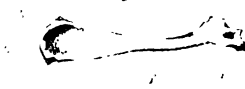


Fig. 3.

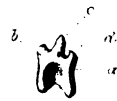


Fig. 4.

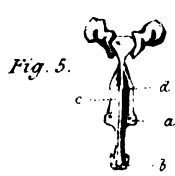


Fig. 5.



Fig. 6.

Fig. 9.

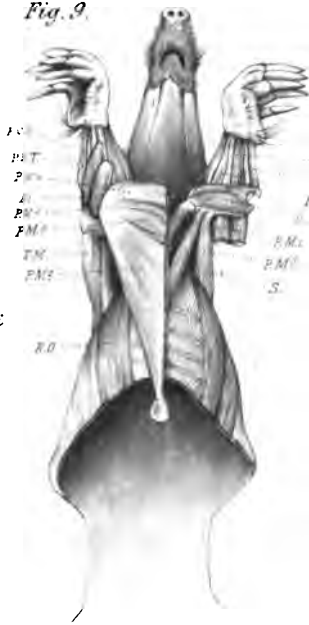


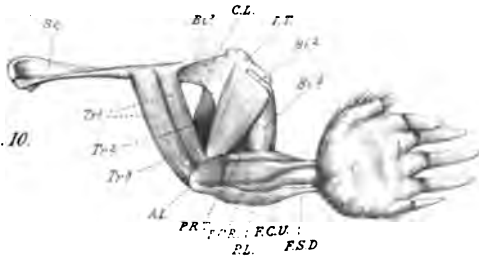
Fig. 7.



Fig. 8.



Fig. 10.



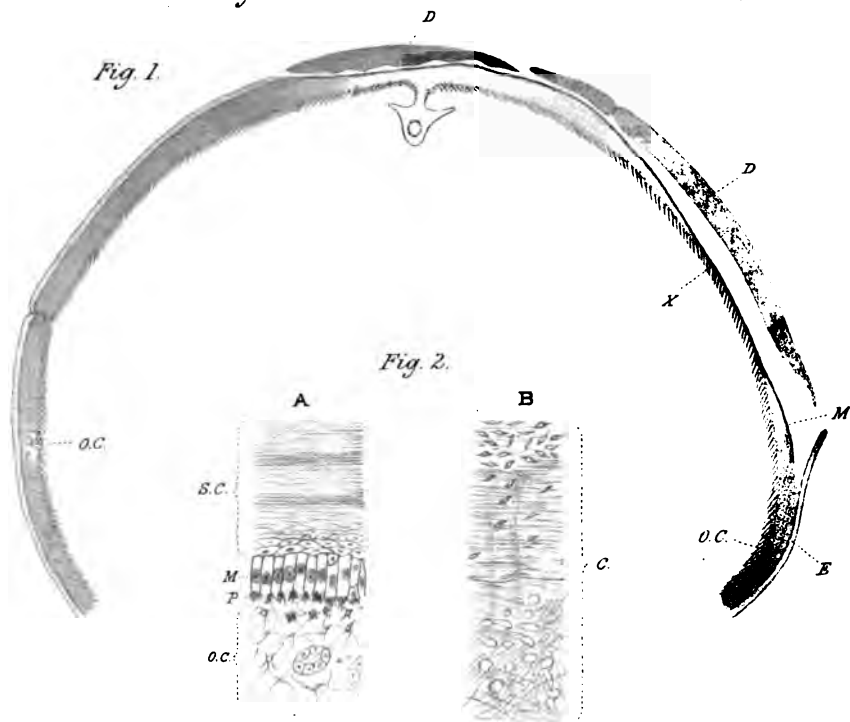


Fig. 3.

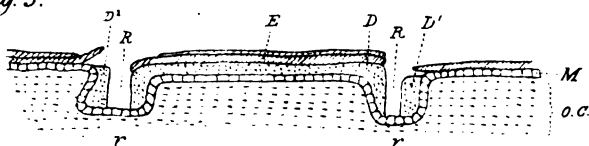
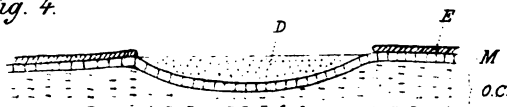
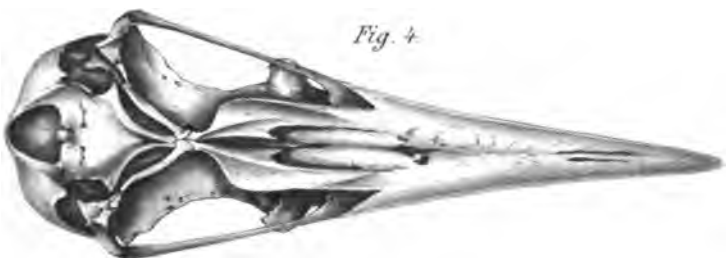
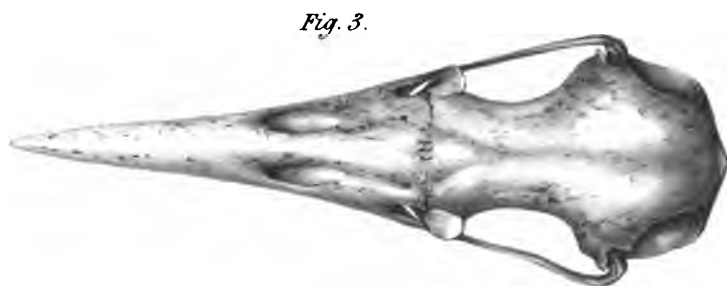
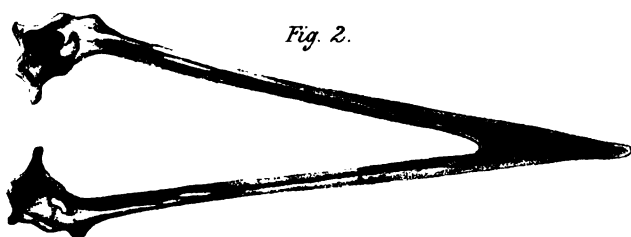
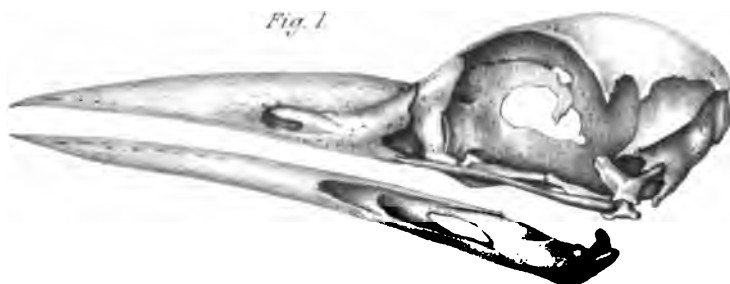


Fig. 4.





P. W. Shufeldt del.

P. Huth Lith. Edin.

GEOCOCCYX.

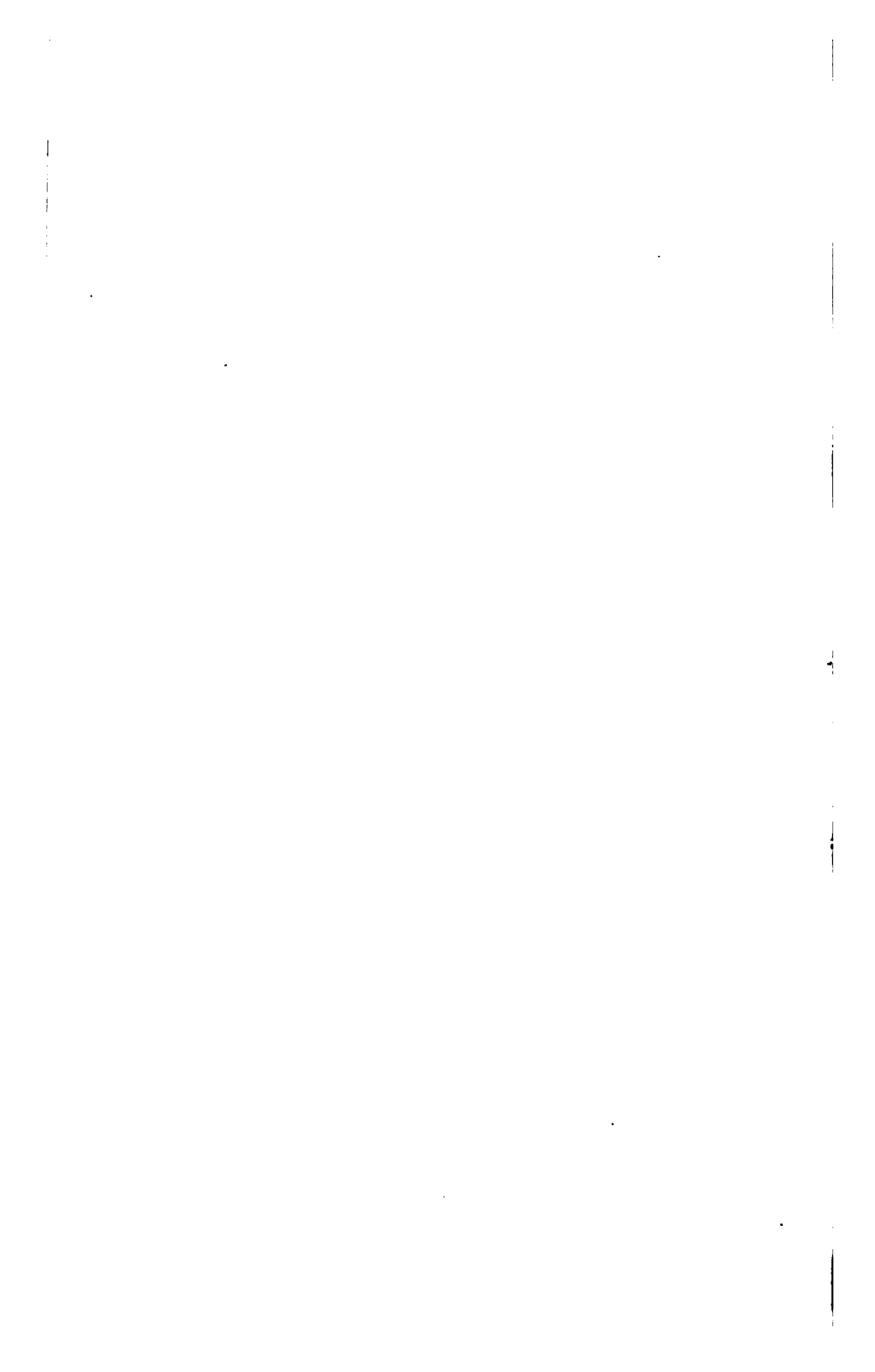


Fig. 5.

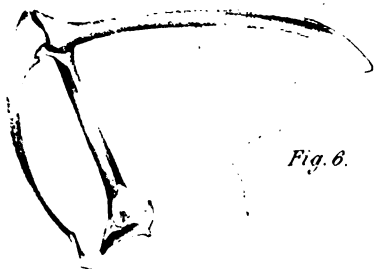


Fig. 6.



Fig. 8.



Fig. 9.

Fig. 7.



Fig. 10.



Fig. 11.



Fig. 12.

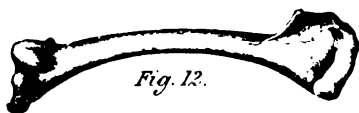


Fig. 13.

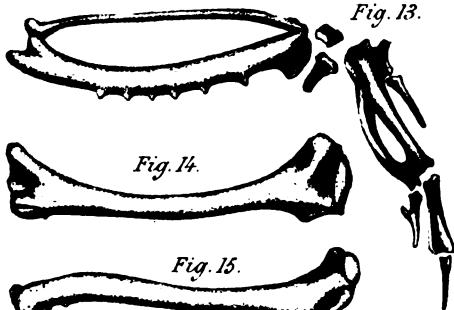


Fig. 14.

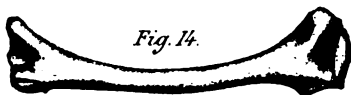


Fig. 15.

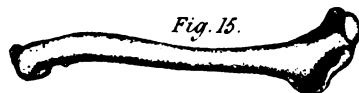


Fig. 16.



R. W. Shufeldt del.

F. Huith, lith^r Edm^d.



Fig. 17.



Fig. 21.



Fig. 22.



Fig. 23.



Fig. 18.



Fig. 19.



Fig. 20.



Fig. 24.



Fig. 27.



Fig. 25.

Fig. 26.



Journal of Anatomy and Physiology.

ACTION OF INFUSED BEVERAGES ON PEPTIC DIGESTION. BY JAMES W. FRASER, M.D., C.M. Ed., M.R.C.S. Eng.

THIS paper is a continuation of that which appeared in the *Journal of Anatomy and Physiology* (vol. xviii. p. 13 *et seq.*), and is based on the results of the same experiments, the difference being that the amount of peptones dialysed, instead of being estimated as the total organic matter, as was done in that paper, is here estimated by the amount of organic nitrogen. It will be found by reference to the earlier paper that, after the various meats had been digested by a peptic fluid in presence of the various beverages, a measured quantity of the filtered solution of peptones was placed in a Graham's parchment paper dialyser, and this suspended in a measured quantity of distilled water for a fixed time. The dialysed matters in solution were then evaporated to dryness in a water bath, a weighed quantity of common salt having first been added to them to make the residue a more manageable substance. Many of these residues had been preserved, the entire quantity not having been used in the former experiments, and it was on these that the experiments to be described were performed. Some of the residues had been entirely used or destroyed, and hence, in comparing the tables appended to this paper with those in the former one, gaps will be found.

A process of estimating the nitrogen, sufficiently accurate to deal with the small quantities available, was much desired from the first, but it was only after many experiments that the following method was arranged and improved until it was satisfactory:—

Small Bohemian glass combustion tubing, about $\frac{1}{4}$ -inch diameter, was taken, and tubes about 4 inches long, drawn out and sealed at one end, were made of it. Into such a tube about 1.5 gram. of the residue was weighed, the tube itself being weighed first and then again after the substance had been placed in it. To this was added four or five times its bulk of powdered recently ignited soda lime, and the tube was plugged with a small piece of recently ignited asbestos. It was then possible by shaking or lightly knocking the tube against a table to thoroughly mix its contents, without the smallest possibility of losing any part of them. The mixed matters should only about two-thirds fill the tube, and when mixed the asbestos should be pressed down the tube until it touches the surface of its contents, and, if necessary, the plug should be pierced with a coarse needle to prevent undue pressure behind it during the combustion, which would burst the tube.

The ammonia given off in the combustion was so small in quantity that no alkalimetric process was sufficiently accurate to estimate the differences between that derived from various samples. A modified Nessler process of estimating the ammonia was therefore employed, and the apparatus used and the method followed were the following:—

The combustion tube was united by a short piece of india-rubber tube to a right-angled glass tube. This was passed through one hole in an india-rubber stopper of size suitable to fit in one of the ordinary Nessler test glasses. The other hole in the stopper was occupied by a large glass tube drawn out below to fit the hole in the stopper, and having its upper part filled with broken glass. The Nessler test glass was filled up to the 50 c.c. mark with distilled water, and the stopper having been inserted, 1 c.c. of the normal volumetric solution of sulphuric acid was poured over the broken glass in the tube above mentioned. As the apparatus behind this tube was air-tight, the acid was retained in the tube. Before heating the combustion tube the india-rubber connection between it and the right-angled tube was protected from the effects of the heat by wrapping a narrow piece of wet linen round it. The upper end of the large tube containing the broken glass and sulphuric acid was connected to a Bunsen filtering pump, which caused a negative pressure of about 4 inches of mercury to be kept up in the whole apparatus, and at once showed if any leakage had occurred, and prevented any loss of ammonia through the leakage. The apparatus having been thus arranged, heat was applied to the combustion tube, and continued until the whole tube was red-hot and the water began to rise in the right-angled leading tube

through absorption of the ammonia. Then a clamp was placed on the tube leading to the filter pump, and the end of the combustion tube was broken off with wet crucible tongs, when the negative pressure existing in the Nessler tube caused a rush of air through the combustion tube, sweeping the last traces of ammonia with it into the water. The combustion tube was then broken off with the wet tongs, between the asbestos plug and the india-rubber connection, and a current of air aspirated through the apparatus by the filter pump to carry any traces of ammonia, not caught by the water, into the broken-glass tube, there to be fixed by the sulphuric acid. The substances operated on not being quite dry, a few drops of condensed moisture were usually found in the horizontal arm of the leading tube, and were washed down into the Nessler glass with a little distilled water. The broken-glass tube, the under surface of the india-rubber stopper, the leading tube, and the walls of the Nessler glass, were then washed with distilled water, and the washings, mixed with the original 50 c.c. of water, were made up to 100 c.c. In the greater number of these experiments the solution thus obtained, though too weak for alkalimetric estimation, was too strong to estimate by Nessler's process, the colour given being too dark for small variations to be easily appreciated. Therefore 25 c.c. were measured out, with a pipette washed with the solution, into another Nessler glass, and this having been made up to 100 c.c. with distilled water, was Nesslerised, and the amount of ammonia estimated in the usual manner.

The process of digestion was described in the earlier paper, and the only reference to it required here is to notice that, when the 75 c.c. of mixed digestive fluid and beverage containing peptones in solution had been filtered, 25 c.c., or one-third of the solution, was used for dialysis. The mixture of salt and dialysed matters obtained by the evaporation mentioned above was weighed, and its weight was called T. The weight of the quantity of the mixed substances taken for combustion was called α , and the amount of ammonia found β .

Then $\frac{T \times \alpha}{\beta}$ = ammonia in T, and $\frac{3T \times \alpha}{\beta}$ = ammonia in the whole

of the 75 c.c. of liquid, and $\frac{3T \times \alpha}{\beta} \times \frac{14}{17}$ = nitrogen in the same amount of liquid, and by this formula the calculations of the experiments were worked out. When, as described above, one-fourth of the solution of ammonia alone was Nesslerised, β was of course obtained by multiplying the amount of ammonia found by 4.

The object of thus re-testing the results of former experiments

was twofold—firstly, to put the conclusions drawn from the total organic solid estimations to the proof, and secondly, to form a link between those experiments and a new series now in course of performance, and for which the old process was found unsuitable.

The conclusions drawn from the experiments on which the first paper is founded may be summarised here, it being premised that they must be taken as applying to experiments performed under the conditions stated in that paper, viz., invariable amounts of meat, digestive fluid, and beverage, and invariable temperature and time of digestion; and that all actions on vital processes of secretion, movement, &c., are eliminated. The conclusions, as stated in the former paper, were the following:—

“(1) All infused beverages retard the peptic digestion of albumenoid food-stuffs, with the four exceptions mentioned above, viz., ham and white of egg with coffee, and fish with cocoatina and with cocoa.

“(2) The digestion of the meats ordinarily used at breakfast, viz., ham, egg, and salt beef, is less retarded by the action of tea or coffee than that of other meats, and the same is true of roast beef; with cocoatina a somewhat similar grouping occurs, but with regard to the other beverages of the cocoa class no such division into a group of breakfast meats, and a group of those less suitable for breakfast use, has been observed.

“(3) That this retarding action is less as a rule with coffee than with tea, and less with either than with the beverages of the cocoa order.

“(4) That the retardation is caused (a) in the case of ‘tea,’ by the tannic acid assisted by the volatile oil, the former precipitating the uncoagulated albumenoids of the food, and the syntonin and peptones as formed, tanning the gelatinous constituents of the meats, and removing some of the pepsin by entangling it with these precipitates, and the latter retarding the action of the pepsin. The alkaloid of tea appears to assist digestion, but its action is masked by that of the tannic acid and volatile oil. (b) In the case of ‘coffee,’ the caffeotannic acid and volatile oil retard digestion, and the alkaloid assists it; and, therefore, in the cases where this beverage assists digestion, the alkaloid must be the active agent in producing the result, and in the cases where digestion is retarded, the caffeotannic acid and the volatile oil. (c) In the case of the cocoas, the tannic acid, volatile oil, and

alkaloid all assist in retarding digestion, but under the conditions of the Standard Process, the clogging action of the suspended matters is the most potent factor.

"(5) In retarding the consumption of acid during digestion tea has the greatest effect, coffee has no more effect than water, and cocoa increases the consumption.

"(6) Coffee and cocoa cause the peptic digestion of albumenoids to pass on through the stage of peptones to the formation of leucine and tyrosine.

"(7) Tea acts on the digestion of fresh meat so as to increase the production of flatus, but has no such effect with salt meat, and coffee has no more effect than water.

"(8) The addition of cream and sugar to the beverages reduces the retarding action of tea on digestion, but increases that of cocoa; and coffee appears to have its action reversed by these additions, but this result is doubtful."

Experiments had been performed (1) on the digestion of beverages alone, these being known as "Factor" experiments, because the result obtained had to be subtracted from the result of the digestion of each meat in presence of that beverage; (2) on the digestion of meats in presence of the beverages called, for the sake of a name, "Peptone" experiments; (3) "Time" experiments, in which the time taken for complete solution of a given quantity of white of egg was the variable on which the conclusions were based; and (4) experiments to ascertain the causes of the effects, noted under the second and third heads. Of the first class, fifteen experiments were performed, but only in nine of these had the mixture of salt and peptones been preserved; tea and cocoatina being among the absentees, new experiments, but made by exactly the old process, were performed, and therefore eleven results are presented in Table B.

Of the second class, fifty-seven experiments had been performed, but of these the residues had only been preserved in thirty-five cases, and no new ones were prepared. Of the third class naturally there was no residue to preserve, and of the fourth class, forty experiments had been performed, but only sixteen residues were preserved, and no new ones were prepared.

Of the above quoted conclusions the first, second, and third were re-tested in these new experiments. Some of the conclusions under the fourth head were also examined, while those under the fifth, sixth, and seventh heads were not meddled with. The eighth set of conclusions were also examined.

Turning now to these new experiments, Table B (Appendix, page 381) is the first to be noted, and consists of three columns, A, B, and C. Column A contains the "Factors" obtained from the digestion of 25 c.c. of each beverage, with 50 c.c. of digestive fluid, the results being estimated by the old process; column B contains the factors expressed as the weight of nitrogen derived from the dialysable organic matter; and column C shows what percentage of this dialysable organic matter consists of nitrogen.

The figures in A and B will be found, as a rule, confirmatory of one another. It is true that three teas, Chinese, Indian, and green, appear to give too small results as compared with the mixed tea, but in most of the others the mutual relations between various sets of figures is maintained in the two columns. In all cases more nitrogen is found where the beverages have been digested than where the digestive fluid has only had water added to it, a result naturally depending on the highly nitrogenised nature of their alkaloids, which more than compensates for any loss of nitrogenous matter from the digestive fluid, by precipitation of albumenoids by the tannic acid or its homologue of the beverages, or by delay produced in digestion by their action.

Turning to the percentage of nitrogen found in the dialysed matter, this is found in the cases of six beverages to fall below that when water is used as the beverage, viz., Chinese, Indian, and green tea, coffee with chicory, cocoatina, and cocoa. In the case of the three last the explanation is simple, the sugar, dialysed with the peptones, being free from nitrogen, naturally reduces the percentage of the latter in the total organic solids. And this is an argument in favour of the nitrogen process in the estimation of peptones, which are thus dissociated from all non-nitrogenised admixture. In the case of the three teas, however, this want of uniformity in their percentages of nitrogen is unexplained by any reason which does not apply to other teas in which the ratio is much higher, and this adds to the suspicion with which these three factors must be regarded.

Infusing tea with alkaline water is seen to extract a rather larger quantity of nitrogenous matter than when plain water is used for infusing the beverage, but the percentage of nitrogen is lower, showing that more hydro-carbonaceous matter (probably

tannic acid uniting with the soda) is extracted in proportion. The nitrogen percentages of mixed tea and of cocoa nibs are both high, showing that these infusions, when properly made, contain much alkaloid and little non-nitrogenised matter. The percentage of nitrogen in the case of coffee is much higher than when chicory is added to it, this, of course, depending on the sugar contained in the latter.

The largeness of these "factors" and their differences among themselves show the necessity of subtracting them from the amounts obtained, when meats are digested in presence of the beverages, in order that serious errors may be avoided. Leaving now the factors, and turning our attention to the second series of experiments, in which 5 gram. of meat were digested by 50 c.c. of digestive fluid, in the presence of 25 c.c. of each of the beverages; the results of these experiments are embodied in Tables D to G inclusive. Table D consists of the results obtained by the estimation of the peptones, obtained by the dialysis of the products of digestion, as organic matter; while Table D₁ is comparable with it, and contains the results of their estimation by the amount of nitrogen they contain, and Table D₂ shows the ratio between the two sets of figures thus obtained, i.e., the percentage of nitrogen contained in the dialysable matters. Table E, extracted like Table D from the former paper, shows the percentage digestive power of each mixture of beverage and peptic fluid, that of water and digestive fluid being taken as 100, and the figures therein contained were obtained by multiplying the result for each beverage by 100, and dividing by the result for that meat digested in presence of water. It is evident that if at the end of the experiment some meat was left undigested, these figures will give the percentage digestive powers of the various mixtures. Table E₁ is one similarly obtained from the nitrogen estimations.

Some irregular results in these experiments were noted in the former paper, and are to be found in Table D.

These consisted of the two minus results—egg digested in presence of chocolate, and bread in presence of the same beverage—but, as these two residues were not among the number preserved, they do not appear in Table D₁, and call for no notice here. The other irregular results were four in number, and

were more noticeable in Table E, where four figures, egg in presence of coffee, ham in presence of coffee, and fish in presence of cocoatina and of cocoa, were found above 100 per cent. The residues of the ham experiments are not among those preserved, nor is that of fish in presence of cocoatina. Therefore, the only two to notice are (1) that of egg in presence of coffee, which receives remarkable confirmation from these new experiments.¹ This result will be seen to have been further confirmed by the "Time" experiments above referred to; and the new series of experiments, of which mention has been made as now progressing, also have the same result. Also, it was noted by Herzen (*Revue Médicale de la Suisse romande, Janvier 1884*) that, in a case of gastric fistula in a man named Band, on whom he made various experiments, café noir assisted the digestion of albumen, though he says tea is without action; a result not in consonance with the experiments here detailed. (2) The other irregular result, fish in presence of cocoa, is not confirmed by these new experiments, which make it appear that cocoa delays, not assists, the digestion of fish. It was said that the result making it appear to assist the digestion of fish was probably fallacious, and these new estimations confirm that view.

But in Table E₁ five more irregular results appear, which were regular in Table E, viz., roast beef in presence of tea, cocoatina, and cocoa, fowl in presence of coffee, and bread in presence of cocoa. As to the first four, nothing can be said except that, possibly the residues not being thoroughly dry, and having been preserved nearly three years in tubes corked securely but only with ordinary corks, some loss of water may have taken place, and thus have caused the rise in the amount of nitrogen. The results in the case of beef were large in the former experiments, but kept below the 100 per cent. In the case of bread digested in presence of cocoa the error is enormous—so great as to bring the percentage digestive power of that mixture up to 464.0 per cent., a result perfectly impossible. The explanation is found in the note appended in Table D to this experiment, which note, though only attached to the cases of chocolate and coffee, really applies more or less to all the bread experiments, and which states that, in the evaporation of the residues some charring occurred.

¹ See Table E₁.

This charring would naturally drive off much nitrogen, and leave a proportionately large percentage of carbon in the residue. Now the bread-cocoa experiment was the least affected by the charring, and hence contained most nitrogen; while the nitrogen in the other cases being reduced to a very small amount, the large result in the case of the least harmed specimen naturally followed. This result, from its obvious falsity, is left out in calculating the average digestive power of a mixture of cocoa and digestive fluid. Again, though no more experiments show such obvious irregularities, yet, on comparing Table E and E₁, the percentages in several cases are found to differ widely in the two tables, though the conclusions to be drawn from the results would be similar in both; that is to say, the results agree in direction, but differ in degree. Some of these differences are probably improvements in the nitrogen estimation, on the results obtained by estimating the total organic solids. Thus the result tea with soda in the Table E gave a high percentage digestive power to the mixture of this beverage and digestive fluid—a result for which no reason could be given, and which is in all probability properly altered in Table E₁. Egg digested in presence of ordinary mixed tea is also considerably altered in position, in the direction of reducing the percentage digestive power of the mixture of beverage and peptic fluid. Again, the smaller percentage in Table E₁ than in Table E in the case of bread-coffee has already been explained. The other differences between Tables E and E₁ are not very enormous, and in all respects, except in the above noted cases, the two tables may be taken as confirming one another. Table D₂ shows the relation between the total organic solid experiments and the nitrogen experiments expressed as the percentage of nitrogen present in the organic matter. This table shows a set of figures acting as a sort of check on the others, for it cannot be conceived that any action of the beverage can split up the nitrogenous matters of the meats so as to cause more or less of the nitrogen to pass through the dialysis paper. Therefore, when any great variation in the percentage of nitrogen is found from that found when water is the beverage, error may be assumed to have occurred either in estimating the nitrogen or the organic matter in the beverage residue or in the water residue. Such very

irregular percentages are found chiefly in the experiments which have been discussed above, such as the case of bread-cocoa, where the percentage of nitrogen is stated to be 28·8, while in the case of bread-water it is only 4·64. Again, egg-water, the percentage is 16·57, while egg-mixed tea gives a percentage of only 9·65, showing that in all probability the amount of organic matter in this case was stated too high, owing to accidents the nature of which was discussed in the former paper. However, in all the more reliable results the nitrogen percentage keeps within limits of variation quite compatible with a fair degree of accuracy in both determinations.

Examining next the average results for digestion in presence of the five principal beverages, which results are found in Tables E and E₁, it is found that by the total organic solids process the beverages in order of action on digestion ran thus:—Water, 100; cocoatina, 89·96; tea, 89·06; coffee, 88·79; Epps' cocoa, 76·05. In the organic nitrogen experiments the order is rather different, being—Water, 100; coffee, 87·32; cocoatina, 87·03; tea, 85·35; cocoa, 80·71. Coffee heads the list of infused beverages, and cocoatina and tea each go down one place. But if the same experiments are selected in both processes for drawing the average, several experiments with each beverage will have to be left out in the total organic solids experiments, and the averages under this head will now stand—Water, 100; tea, 92·06; coffee, 87·56; cocoatina, 81·68; and cocoa, 75·8. Cocoa stands lowest in all three; but while cocoatina heads the list of averages in the first set, it sinks to the second place in the nitrogen experiments, and to the third in the last set of averages. Coffee heads the list in the nitrogen averages, is second in the last list, and third in the first list. Now, as was remarked in the former paper, cocoatina headed the list of averages owing to the persistently moderate results it gave; while tea and coffee, though they had various very high results, were brought down by others which were very low. Now it happens in the case of tea that those residues which were preserved were chiefly those giving high results; and hence in the nitrogen averages and the total organic solid average of the same experiments, tea takes a higher place. Coffee in this latter set of averages is reduced to the third place, because some

of its highest results, ham, salt beef, and fish have to be omitted, and it is brought to the head of the nitrogen averages by the irregular result with roast fowl. The less important beverages take the following order in the total organic solids experiments—Tea with soda, 97; cocoa nibs, 78·8; Chinese tea, 72·8; coffee with chicory, 62·9; green tea, 51·6; and Indian tea, 45·4. In the nitrogen experiments the order is—Chinese tea, 74·27; coffee with chicory, 69·35; cocoa nibs, 66·69; green tea, 66·14; Indian tea and tea with soda, 62·98. Tea with soda has in the nitrogen experiments to leave the head of the list and join Indian tea at the foot, while cocoa nibs infusion has to yield two places. The rest of the beverages follow the same order in both sets.

Examining individual results in the cases of the principal beverages, it was found in the former paper that the meats grouped themselves, as regards the effect of the beverages on their digestion, into a set less injuriously affected, called breakfast meats, and a set more injuriously affected. In the case of tea, the less affected meats were—roast beef, 96·4 per cent.; salt beef, 94·8 per cent.; ham, 95·98 per cent.; and white of egg, 91·7 per cent.; and the more affected—fowl, 66·73 per cent.; lamb, 88·4 per cent.; fish, 88·26 per cent.; and bread, 89·23 per cent. In the nitrogen experiments the higher set contains—roast beef, 125·71 per cent.; salt beef, 84·24 per cent.; and bread, 89·68 per cent.; and the lower—fish, 72·35 per cent.; and egg, 54·8 per cent.; while lamb, ham, and fowl are wanting. Here roast beef and salt beef on the one hand, and fish on the other, remain in the same sets in both estimations, while egg and bread have changed places. But bread is in both cases a doubtful experiment, especially in the nitrogen estimations, for reasons above alluded to.

For coffee the total organic solid results gave a higher division, consisting of—egg, 106·45 per cent.; ham, 100·44 per cent.; roast beef, 98·8 per cent.; fish, 96·33 per cent.; and salt beef, 93·4 per cent.; and a lower—bread, 58·27 per cent.; lamb, 69·95 per cent.; and fowl, 86·74 per cent. The nitrogen results are, in the higher set—egg, 109·1 per cent.; roast beef, 97·18 per cent.; and fowl, 104·74 per cent.; and the lower set only contains the suspicious bread, 38·28 per cent., here agreeing with

the organic solid result; salt beef, lamb, ham, and fish are wanting, and fowl has passed from the lower into the higher set. With cocoatina the division into two classes is less evident, the higher class containing, in the former experiments—fish, 139·77 per cent.; egg, 85·25 per cent.; roast beef, 88·09 per cent.; salt beef, 86·88 per cent.; ham, 88·96 per cent.; and bread, 87·22 per cent.; and the lower—lamb, 77·04 per cent.; and fowl, 66·52 per cent. In the nitrogen experiments the higher set contains—egg, 96·10 per cent.; roast beef, 110·42 per cent.; salt beef, 83·81 per cent.; and the lower—fowl, 57·82 per cent.; lamb, ham, and fish being wanting, but all those which remain occupying the same places in both estimations. In the case of cocoa, no order or arrangement could be detected in the former experiments, and the same is the case here. The higher set—roast beef, 110·9 per cent.; fish, 82·65 per cent.; bread, 464·0 per cent.; and the lower—egg, 59·79 per cent.; salt beef, 69·52 per cent.; lamb, ham, and fowl do not appear. Examining the figures in the case of tea, coffee, and cocoatina, the notable differences produced by the two methods of estimation are—(1) white of egg having passed in the lower set in the case of tea, and fowl into the higher in the case of coffee. The results with roast beef in the cases of tea and cocoatina are much larger in the nitrogen than in the other estimations, but remain in the same division. Summing up these results, it may be stated that the meats least acted on in digestion by tea, coffee, and cocoa are roast beef and salt beef; that if ham were not wanting in the nitrogen results it would probably come into the list; and that egg is little acted on by cocoatina, and its digestion positively assisted by coffee, while tea retards its digestion. The positions of bread and fowl in the higher list in the nitrogen estimations, and of fish in the same list in the organic solid estimations, are doubtfully correct. Thus these new estimations confirm the remarks made about the older set, that the common use of salt beef, ham, and egg, as well as of roast beef, as breakfast dishes—that is at the only meal at which custom sanctions the mixture of infused beverages and meats—is founded, probably unwittingly, on scientific principles.

Experiments called "Time" experiments have been mentioned above, and were described in the former paper. In these

the percentage digestive powers of the mixtures of beverages and digestive fluid were calculated from the time required for complete solution of a fixed quantity of white of egg. In Table G, column A, the percentage digestive powers thus calculated are shown; in column B the percentage digestive powers are calculated from the "Peptone" experiments with white of egg, see Table E; in column C from the averages of the peptone experiments; in column D from the same experiments as in B, but calculated from the nitrogen estimations; and in column E as in C, but also calculated from the nitrogen estimations. Here in the case of tea the difference between the total organic solid and the nitrogen estimation of its action with white of egg is seen, while the average results with this beverage agree pretty well with each other and with the "Time" result. In the case of coffee this is reversed, the averages agreeing with each other but disagreeing with the Time experiment, which comes nearer to the estimations with white of egg only. This, of course, depends on the fact that coffee assists the digestion of white of egg, but retards more or less that of other meats.

In the cases of cocoatina and cocoa the figures in each of the columns agree pretty well one with another, and as no nitrogen estimations were made with chocolate no notice need be taken of it.

Summing up the results, very similar words may be used to those used in the former paper: (1) that all infused beverages retard the digestion of all meats, with five exceptions, these being white of egg with coffee, and perhaps fowl with coffee, and roast beef with tea, cocoa, and cocoatina; (2) under this general rule some subdivisions must be noticed; thus tea has less action on roast beef and salt beef and doubtfully on bread; and coffee has less action on roast beef and assists the digestion of white of egg, and perhaps of fowl; and again, cocoatina has less action on the digestion of egg and of salt beef, and appears to assist the digestion of roast beef; while with cocoa no subdivision into two classes can be traced.

The results obtained in the former estimations, and which have been, as a rule, confirmed by the later detailed here, having been examined, some attempts were made to arrive at their causes by the performance of various special experiments.

The results of the "Cause" experiments were re-tested, in the suitable cases which remained, by the nitrogen process.

One of the theoretical causes which might assist in producing the retardation of digestion by various of the beverages was the fact that precipitates formed in the digestive fluids by tea and cocoa (coffee gave no such precipitate) would carry down pepsin entangled with them (according to a well-known property of this ferment), and this pepsin would not be entirely re-dissolved during digestion. This theoretical consideration was put to the practical test by the experiments, the results of which appear in Tables H, I and I₁. In Table H factors are shown obtained by digesting mixtures of beverages and digestive fluid (mixed in the proper proportions), but which mixtures had been filtered before digestion, thus preventing any resolution of the pepsin. The removal of the pepsin in the case of tea is equivalent to a loss .001 grm. of organic matter, or .0022 grm. of organic nitrogen, the loss of nitrogen being slightly greater in proportion than that of organic matter, as will be seen by comparing the percentage of nitrogen in this table with that in Table B. In the case of coffee, where no precipitate formed, the deviations are trifling and irregular, and depend on experimental errors. In the case of cocoa, the removal of the suspended matters of the beverage from the action of the digestive juice reduced the factor in column A from .53 grm. to .412, while the nitrogen factor in column B is practically the same in both cases, the difference being only .0004 grm. of nitrogen, and this in favour of the filtered solution, showing that little if any pepsin is removed by the cocoa precipitate, and also that the substances extracted by digestion from the suspended solids must chiefly consist of non-nitrogenous matter, such as tannic acid, sugar, &c., this being shown by the nitrogen percentage being higher in the case of the filtered than of the unfiltered beverage.

When white of egg is digested in presence of these beverages, filtered after mixing with the digestive fluid, it is found, as might be expected, that but little different effect is produced in the case of coffee, whether filtered or not, the percentage digestive power in the former case being 108.33, in the latter 109.10. In the case of cocoa a wide difference is observed

between the results with the filtered and unfiltered beverage, the digestive power in presence of the former being 209.45 per cent., of the latter 59.79.¹ The former large result in the estimation by the nitrogen process is similar in direction, but widely different in degree, from that in the total organic solid estimation, viz., 126.03 per cent., but both of these depend, not on any action of the infusion itself, but on the removal of the suspended matters, which, falling to the bottom of the beaker used in the digestive operations, coated over the white of egg, and prevented the digestive fluid from acting on it.

No nitrogen estimation in the case of white of egg, digested in presence of a mixture of tea and digestive fluid, filtered after mixing, was made, but from the agreement between the organic solid and the nitrogen "Factors" for this mixture it may be assumed that the organic solid experiment, in the case of egg, would have been confirmed by the nitrogen experiment.

The second theoretical cause, viz., the contraction by the gelatinous matters of the meat by the tanning action of tea and cocoa; and the third, viz., coagulation of any albumenoids of the meat by the action of any of the beverage, rest solely on the total organic solid estimations, no new estimations having been made.

The same is true of the fourth possible cause, viz., the retarding action of the volatile oils on digestion; and of the fifth cause, viz., the action of the alkaloids, which was shown in the case of theine or caffeine to be favourable to digestion. The sixth possible cause, viz., the precipitation of syntonin and peptones as formed,¹ by the tannic acid or its homologue present in the beverage, was re-tested as far as the syntonin is concerned, the results of both estimations being shown in Tables N and N₁; the process, detailed in the former paper, consisted in mixing 25 c.c. of a solution of syntonin with 25 c.c. of a digestive fluid of double strength, thus giving an unknown but invariable quantity of syntonin, dissolved in a digestive fluid of the normal strength; to this 25 c.c. of the beverage was added, and digestion and the remainder of the process carried out.

The total organic solid estimations show a great reduction of the amount of syntonin converted into dialysable peptones in the

¹ See Table E₁.

case of tea and coffee, the amounts dialysed being only 14.6 and 17.4 per cent. respectively, of what passed through when water was the beverage, but with cocoa the reduction is only to 50.9 per cent. The nitrogen estimations, though all agreeing in kind with these, vary much in degree; thus the result for tea is a minus quantity, that is to say, not enough nitrogen was dialysed to supply the whole nitrogen factor in tea. With coffee, again, the percentage of nitrogen dialysed was 76.54 per cent. of that dialysed in presence of water as the beverage. This agrees better with what has already been shown of the action of coffee on digestion, and may probably be more correct than the organic solid estimation. With cocoa the percentage is only 19.34, which may or may not be more correct than the organic solid percentage.

The seventh possible cause applies only to beverages containing much albumenoid matter, and is that the accumulation of peptones from this albumenoid matter may arrest the digestive power of the pepsin. No special experiment on this was performed, but as confirming the principle, attention may be called to the figures for digestion of white of egg and beef in undiluted digestive fluid, Tables D to E₁. The superiority in accuracy of the nitrogen process over the organic solid process of estimation is well shown in the case of these two results in Table E₁, where, instead of disagreeing by more than 12 per cent., as they do in Table E, they agree within .2 per cent., a result which is evidently correct, as they depend on a property of the digestive fluid. They show that reducing the amount of water in the digestive fluid by one-third reduces its peptonising property by almost exactly the same amount. The eighth and last possible cause has already been referred to, and is that the suspended matter of beverages like cocoa clogs the action of the digestive fluid. As an example of this the action of cocoa on digestion before and after filtering may be referred to. Summing up the causes of the action of the beverages on digestion, so far as they have been re-tested by the nitrogen process of estimation, it is found—

(1) That tea, as a type of all the "teas," retards digestion as a rule, and acts by causing precipitates which entangle and carry down the pepsin, and by precipitating the syntonin as

formed in digestion. It was shown further in the former experiments that it was chiefly the tannic acid which had these properties, and that it also acted by precipitating the peptones as formed and by tanning the gelatine and albumenoids of the meats; that the volatile oil also had some action in reducing digestion; and that the action of the alkaloid, if any, was favourable to digestion.

(2) The action of coffee, taken as a type of the "coffees," depends on the action of its caffee-tannic acid in retarding digestion by various of the above actions. It has been seen from the nitrogen results that coffee does not act by precipitating pepsin, and that it has less action than the other beverages in precipitating syntonin. When coffee assists digestion it appears from the former estimations that the alkaloid is the active ingredient.

(3) Cocoa has been shown by the nitrogen experiments to precipitate syntonin as formed, and also, by the clogging action of its suspended matter, to reduce the activity of digestion. This latter action would in all probability not occur in the stomach, the active movements of which would prevent this stagnation. In respect of the other actions, the results of which were not re-tested by the nitrogen process, it is intermediate in activity between tea and coffee; and further, its alkaloid appears slightly to retard digestion.

The first, second, third, and fourth of the conclusions quoted above have been reviewed, and as the fifth, sixth, and seventh left no results to re-test, there only remains the eighth and last, viz., that relating to the effects, on the actions of beverages on digestion, of the addition to these beverages of milk and sugar, in proper proportions. To the 25 c.c. of beverage, 5 c.c. of milk and 2.15 gram. of sugar were added. Factor experiments were performed without meat, their results being found in Table R, where column A contains the total organic solid estimations, B the nitrogen estimations, and C the percentage of nitrogen in the former results.

It was found by the organic solids process that tea slightly reduced the amount of dialysable matter produced in the digestion of the milk as compared with the results where water was the beverage, coffee somewhat increased the amount, and cocoa increased it considerably. In the nitrogen results it is

found that the result with tea is slightly greater than that with water, and that the percentage of nitrogen is also greater, pointing to the fact that the nitrogen of the alkaloid is more than sufficient in this to make up for any loss of albumenoids from the milk or the digestive fluid. In the case of coffee, the nitrogen result, though considerably greater than that with water as the beverage, still has the nitrogen percentage somewhat smaller than with tea, though very slightly. In the case of cocoa the percentage of nitrogen, more than one per cent. higher than in any other case, is suspicious for the accuracy of this result. The smallness of these percentages of course depends on the large quantity of sugar in the dialysed matters.

The results of digestion of white of egg with peptic fluid, in presence of water alone, and of the three typical beverages, with milk and sugar, are shown in Tables S and S₁.

The nitrogen estimations all agree in direction with those obtained by the organic solids process, but differ greatly in degree. The result with coffee confirms what was said in the former paper, that the addition of milk and sugar to this beverage reverses its action on the digestion of white of egg. In the case of cocoa the addition of milk increases its action on digestion by increasing the amount of suspended matter, which covers over the meat, and by increasing the amount of albumenoid matter in the beverage, which, by becoming peptonised, reduces the action of the peptic fluid on the meat. Therefore the minus result in this case is not without probability. But tea was believed from the former experiments to have its retarding action on digestion lessened by the mixture with it of milk and sugar. This is not confirmed by the nitrogen results, and therefore the real effect of milk and sugar on the action of tea on digestion remains for the present doubtful. Reverting to the conclusions of the former paper, it is found that the first conclusion, viz., that all beverages retard the peptic digestion of all albumenoid food-stuffs, is confirmed, but the exceptions are rather different, being in the new estimations white of egg with coffee; roast beef with tea, cocoatina, and cocoa; and fowl with coffee. Fish with cocoa ceases to be an exception to the rule; and ham with coffee, and fish with cocoatina, were not examined.

(2) The grouping into breakfast meats is more or less retained in the cases of tea, coffee, and cocoatina, but white of egg is removed from this group in the case of tea. Cocoa, as before, shows no such grouping.

(3) This retarding action is less with coffee than with tea as a rule, and less with either of these than with the cocoas.

(4) As to the causes, the only ones examined in these new estimations were the precipitation of syntonin by the tea and the precipitation of pepsin by the precipitates caused by the tea; the occurrence of these causes of retardation being confirmed. The action of caffee-tannin in these directions was shown to be slight, and the same was shown to be true with regard to the tannic acid of cocoa. The principal cause of the action of cocoa on digestion was shown to be the clogging action of its suspended matters. Therefore the causes of the actions of the beverages, as shown by the organic solids process, are confirmed by the nitrogen process in the cases in which they were re-tested.

(8) The addition of milk and sugar to cocoa was shown to increase its retarding action on digestion, and the reversal of the action of the coffee by these additions was confirmed. But no confirmation was given of the result with regard to tea obtained in the former estimations.

In the former paper certain practical deductions from the experimental results were drawn, but as these remain the same under the new estimations it is unnecessary to recapitulate them here. One conclusion, however, deserves reference, viz., the large loss which results from eating meat and drinking infused beverages at the same time.

Sir L. Playfair quotes as a mere "subsistence" diet that of a London sempstress, and states that it consists of—

Nitrogenous matter,	2.33 oz. or 65.95 grm.
Fat,	0.84 oz. or 23.8 grm.
Carbohydrates,	11.69 oz. or 331.4 grm.

the food being reckoned as dry solids. This diet, excluding fats, would be represented by—

Bread,	19.3 oz. or 550 grm.
Meat,	10.5 oz. or 300 grm.

reckoned as they appear as food and containing water. It

TABLE D.

Results of the peptone experiments.

	Bolled White of Egg.	Roast Beef.	Bolled Salt Beef.	Roast Lamb.	Bolled Ham.	Roast Fowl.	Bolled Fish.	Bread.
	Grms.	Grms.	Grms.	Grms.	Grms.	Grms.	Grms.	Grms.
Digestive fluid undiluted,	376a	771b
" with water,	434a	1-042b	1-121	649	697	920	792	446
" with mixed tea,	398	1-005b	1-063	574	661	614	639	396
" with Chinese tea,	317
" with Indian tea,	197
" with green tea,	224
" with tea with soda,	421
" with maté,	359
" with coffee,	462a	1-03c	1-047	454	501	796	763	26d
" with coffee and chicory,	273
" with Arab coffee,	295
" with coccoatins,	390	918c	974	500	796	613	1-107	389
" with cocoa,	164	815c	973	542	628	..	812	330
" with chocolate,	005	..	588	407	646	795	700	-058d
" with cocoa nibs,	248
" with guarana,	224

Results marked (a) belong to a different set from the rest of the experiments with white of egg. Results marked (b) belong to a different set from those marked (c) in the experiments with roast beef.

(d) Charring took place in the evaporation of the dialysate in these cases.

TABLE D₁.

Results of peptone experiments estimated as organic nitrogen.

	White of Egg.	Roast Beef.	Bolled Salt Beef.	Roast Lamb.	Bolled Ham.	Roast Fowl.	Bolled Fish.	Bread.
	Grms.	Grms.	Grms.	Grms.	Grms.	Grms.	Grms.	Grms.
Digestive fluid undiluted,	0519	1084
" with water,	0719	1497	2101	1305	1306	0206
" with mixed tea,	0394	1882	177	0945	0945	0185
" with Chinese tea,	0534
" with Indian tea,	0453
" with green tea,	0476
" with tea with soda,	0453
" with coffee,	0785	1455	..	0999	..	1405	..	0079
" with coffee with chicory,	0499
" with coccoatins,	0691	1653	176	1146	..	0780
" with cocoa,	0430	1660	1461	0965	1079	0958
" with cocoa nibs,	0480

TABLE D.

Percentage of nitrogen in the total organic solids results.

	White of Egg.	Roast Beef.	Boiled Salt Beef.	Roast Lamb.	Boiled Ham.	Roast Fowl.	Boiled Fish.	Bread.
	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.
Digestive fluid undiluted,	18.81	14.05						
" with water,	16.37	14.36	18.75			14.67	16.48	4.64
" with mixed tea,	9.65	17.17	16.65				13.5	4.65
" with Chinese tea,	16.84							
" with Indian tea,	23.00							
" with green tea,	21.20							
" with tea with soda,	19.75							
" with coffee,	16.99	14.12		21.99		14.28		8.03
" with coffee with chicory,	18.31							
" with cocoasina,	17.71	18.00	18.05	22.92		12.75		
" with cocoa,	26.24	20.07	18.00	17.80			13.29	28.8
" with cocoa nibs,	19.75							

TABLE E

Percentage results of the peptone experiments.

[illegible]

TABLE E₁.

Percentage results of peptone experiments estimated by nitrogen process.

	White of Egg.	Roast Beef.	Boiled Salt Beef.	Roast Lamb.	Boiled Ham.	Roast Fowl.	Boiled Fish.	Bread.	Average.
	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.
Digestive fluid undiluted	72.21	72.42							72.31
" with water, . . .	100	100	100	100	100	100	100
" with mixed tea, . .	54.80	125.71	84.24	73.35	69.68	85.35
" with Chinese tea, . .	74.27	74.27
" with Indian tea, . .	62.98	62.98
" with green tea, . .	66.14	66.14
" with tea with soda, .	62.98	62.98
" with coffee, . . .	109.10	97.18a	..	104.74	..	38.28	87.32
" with coffee and chicory, .	69.25	69.25
" with cocoatina, . .	96.10	110.42	83.81	..a	..	87.62	87.03
" with cocoa, . . .	59.79	110.9	69.52	..a	83.65	444.06	80.71
" with cocoa nibs, . .	66.69	66.69

a. Absent because there is no water experiment for comparison.

b. Omitted in calculating average.

TABLE G.

Percentage digestive powers of mixtures of digestive fluid and beverages deduced—A, from time experiments; B, from peptone experiments with white of egg; C, from average of peptone experiments; D, from nitrogen experiments with white of egg; and E, from average of nitrogen experiments.

	A.	B.	C.	D.	E.
	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.
Digestive fluid with water, . . .	100	100	100	100	100
" with mixed tea, . . .	89.26	91.7	89.06	54.80	85.35
" with coffee, . . .	115.02	106.45	88.79	109.10	87.32
" with cocoatina, . . .	72.04	85.25	89.96	96.10	87.03
" with cocoa, . . .	89.26	37.78	76.05	59.79	80.71
" with chocolate, . . .	76.23	..	72.44

[TABLE H.]

TABLE H.

Results of digestion of 50 c.c. of digestive fluid with 25 c.c. of the three principal beverages, filtered after mixing. A, Total organic solid estimations; B, Organic nitrogen estimations; C, Percentage of nitrogen in organic solids.

	A. ;	B.	C.
	Grms.	Grms.	Per cent.
Mixed tea,	·225	·0221	10
Coffee,	·263	·0263	10
Cocoa,	·412	·0301	7·3

TABLE I.

Results of digestion of 5 grms. white of egg with 50 c.c. of digestive fluid, and 25 c.c. of beverage, filtered after mixing.

	Actual Weights.	Percentages.
	Grms.	Per cent.
Water,	·434	100
Mixed tea,	·34	78·34
Coffee,	·462	106·45
Cocoa,	·547	126·03

TABLE I₁.

Results of digestion of 5 grms. of white of egg with 50 c.c. digestive fluid and 25 c.c. of beverage, filtered after mixing. Results estimated by nitrogen process.

	Actual Weights.	Percentages.
	Grms.	Per cent.
Water,	·07195	100
Mixed tea,
Coffee,	·07795	108·33
Cocoa,	·1506	209·45

TABLE N.

Digestion of syntonin in presence of water, and of the three principal beverages.

	Actual Weights.	Percentages.
	Grms.	Per cent.
Water,	·1206	100
Mixed tea,	·0176	14·6
Coffee,	·021	17·4
Cocoa,	·0615	50·9

TABLE N₁.

Digestion of syntonin in presence of water and of three principal beverages. Estimated by nitrogen process.

	Actual Weights.	Percentages.
	Grms.	Per cent.
Water,	·0162	100
Mixed tea,	·00649	...
Coffee,	·0124	76·54
Cocoa,	·0031	19·34

TABLE R.

Results of digestion of 25 c.c. of beverage, with 5 c.c. of milk and 1·25 grm. of sugar, in presence of 5 c.c. of digestive fluid. A, total organic solid estimations; B, organic nitrogen estimations; C, percentage of nitrogen in organic solids.

	A.	B.	C.
	Grms.	Grms.	Per cent.
Water,	1·345	·0309	2·29
Mixed tea,	1·275	·0324	2·54
Coffee,	1·413	·0356	2·52
Cocoa,	1·677	·0619	3·69

TABLE S.

Results of digestion of 5 grms. of white of egg in presence of water, and of the beverages with milk and sugar.

	Actual Weights.	Percentages.
	Grms.	Per cent.
Water without milk,	·434	100
Tea with milk and sugar,	·426	98·15
Coffee with milk and sugar,	·237	54·6
Cocoa with milk and sugar,	·04	9·2

TABLE S₁.

Results of digestion of white of egg in presence of water, and of the beverages with milk and sugar. Estimated by nitrogen process.

	Actual Weights.	Percentages.
	Grms.	Per cent.
Water without milk, &c., .	·07195	100
Tea with milk, &c., . .	·0189	26·31
Coffee with milk, &c., . .	·0154	21·37
Cocoa with milk, &c., . .	- ·00546	...

SOME VARIATIONS IN THE HUMAN SKELETON. By
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*Asymmetry of the Spinal Column, Chest, and Skull; Bifid Ribs
and Cartilages; Extent of Lower Limit of Pleura, &c.*

I WILL give a detailed account of these cases, and note the variations from the normal as they occur, discussing any points of interest in connection with them.

The first case was a man about 5 feet and 8 inches in height, with a chest of average size. His sternum was abnormally thick and broad. The greatest breadth of the manubrium was $3\frac{1}{8}$ inches, and the least $2\frac{1}{4}$ inches. The greatest breadth of the gladiolus was $1\frac{1}{2}$ inches. The length of the manubrium was $2\frac{3}{8}$ inches, that of the gladiolus $4\frac{1}{2}$ inches. They were united to one another by a thin layer of dense fibrous tissue, the joint so formed allowing of very slight movement.

The first ribs were almost exactly symmetrical in size and in position. The span of each was $3\frac{1}{2}$ inches. The first cartilage was placed a little more horizontally than usual; its antero-posterior diameter was unusually great, and it was more than normally flattened on its upper surface. It was ossified in almost the whole of its thickness. In each an amphiarthrodial articulation was present. On the right side it was situated in its usual position, namely, half an inch from the extremity of the rib; and on the left side it was placed in the centre of the ossified cartilage. The other costal cartilages were quite free from any ossific change. Owing to a slight obliquity of the articulation between the two pieces of the sternum, the left second costal cartilage was attached to the sternum at a slightly higher level than the right.

The third right costal cartilage was nearly normal in depth at its attachment to the sternum. As it passed outwards it rapidly increased in vertical measurement, and just before its junction with the correspondingly enlarged extremity of the third rib it was perforated by a foramen $\frac{5}{8}$ inch in diameter. At this point the cartilage was $1\frac{1}{2}$ inches deep.

The third left costal cartilage was about $\frac{3}{4}$ inch deep, and was attached to the sternum a little above its fellow.

The right fourth cartilage was normal throughout.

The left fourth cartilage was $1\frac{1}{2}$ inches deep at its inner end, where it was perforated by a foramen half an inch in diameter. Its depth diminished as it passed outwards, though it had not reached its normal measurement where it joined the enlarged extremity of the fourth rib.

The right fifth cartilage was nearly an inch deep in the greater part of its length, though at its inner end it was somewhat narrower.

The left fifth cartilage was $\frac{3}{8}$ inch deep, and attached to the sternum above its fellow.

The right sixth and seventh cartilages were normal, and articulated with the sternum.

The left sixth cartilage was $1\frac{1}{2}$ inches deep at its inner end. It increased considerably in breadth as it passed outwards, and at a point $1\frac{1}{2}$ inches from the sternum it split into two cartilages, which enclosed a foramen measuring $3\frac{1}{2}$ inches in its transverse diameter. These two rods of cartilage united with the bifurcated broad extremity of the sixth rib, which itself bounded the foramen.

The seventh left cartilage was broader than usual and articulated with the sternum. A point of some clinical interest was the very narrow interval in the front side of the chest between the left sixth rib and cartilage and the adjoining ribs and cartilages, especially the seventh. This circumstance would have caused some inconvenience in the event of the ordinary operation for an empyæma being performed here, as it would have been impossible to drain the cavity through such a narrow interspace without resecting a portion of the rib.

The left costal cartilages articulating with the sternum were, with the exception of the first, at least a quarter of an inch longer than those of the right side.

The bones forming the spinal column were dense and strong. They presented no lateral curve or extensive pressure change. The upper dorsal vertebræ were thrown slightly forwards. There were no old pleuritic adhesion or chronic lung affection. There was the same condition of the vertebræ which was present in a case I described in the last volume of the *Jour. of Anat. and Phys.*, "Vertebral Asymmetry," &c. Up to the present time that case was the only instance of vertebral asymmetry I have seen in the dissecting room which was not due to pressure or costal leverage. In this case the left transverse processes were directed in a more upward and backward direction than usual, so that on this side there was a narrower groove between the transverse processes and spines than on the opposite side. The difference on the left side, on an average, was about half an inch in the middle eight dorsal vertebræ, and about an eighth of an inch in the upper two dorsal vertebræ. The left were also on a higher level than the right. This difference in level in the upper and central part of the dorsal spine varied from about half an inch to about a quarter or an eighth of an inch in the lower dorsal vertebræ.

Chiefly on account of the alteration in the direction of the left transverse processes, but slightly also owing to a diminution in the length of the ribs between the angles and heads, their angles of the ribs on the right side were more distant from the middle line than those on the opposite side. This difference amounted in some to half an inch, and in others to three-quarters of an inch. In this chest we have, besides a certain amount of asymmetry in the attach-

ment of the costal cartilages to the sternum, asymmetry in the form and length of the cartilages and ribs, and of the laminæ and transverse processes of the dorsal vertebrae.

One would have expected the cartilages on the left side to be the shorter, as they are attached to the sternum at points higher than their fellows. This asymmetry of the two sides of the chest is very interesting, both from a clinical as well as from an anatomical point of view; and, as I have already shown in previous papers, it is by no means an uncommon condition.

I would here protest strongly against the clinical habit of gauging too accurately the size of the heart by the relation borne by the apex-beat to the nipple and to the interspace. The chest wall is frequently so variable in its bony framework that, in a doubtful case, its constituent parts should be carefully defined and measured, and a broad margin allowed for the position of the healthy apex, should the framework of the chest deviate to any great extent from what is regarded as the normal, or to speak more accurately, the more common type. The more I examine the bodies of subjects in the dissecting room, the more am I convinced of the importance of this fact, and I do not think it is sufficiently recognised, if it is so at all, by clinical observers.

It is also by no means uncommon to find considerable asymmetry of the skull. In the case that I have just described the skull was nearly symmetrical, the left half being slightly the larger of the two. It is curious that the cavity of the skull should be so frequently asymmetrical, and yet it is not so difficult to attempt an explanation in the case of the skull as it is in the case of the framework of the chest. I have examined and measured a number of skulls, and in the large majority I have found the left half to be larger than the right. I measured them by stretching a string from the skull immediately above the crista galli to a point immediately above the centre of the longitudinal sinus at the internal occipital protuberance, the skull cap having been removed in the usual way. At right angles to this, other cords were stretched, and the distances from the middle line measured. As a rule, the increase was tolerably general on one side, but in many cases it was limited to the front or back of the skull. Given that one half of the cavity is larger than the other, I think we may assume that the half

of the cerebrum contained in it is also larger than the other half.

As the right limbs have for generations been used much more extensively than the left, not only in obedience to very complicated efferent impulses, but also, in the hand especially, for the purpose of gathering afferent impulses of a very complex nature, it is I think fair to suppose that, as the result of this, the left half of the brain has become larger than the right. I hope soon to have more accurate data as to the relative frequency of the side and portion of the side enlarged.

In torticollis occurring at an early period of life, we see what appears to be an atrophic or a less developed condition of the head and face on the affected side. This does not seem to be explicable on the same physical basis as are the curves and changes produced in the spinal column, and the consequent alterations in the form of the chest. I have not yet been able to examine the skeleton of a subject affected by torticollis accompanied by asymmetry of the skull and face, though I was fortunate in being able to examine the bodies of two adults in whom the cranial changes were not present. One is described in the *Transactions of the Pathological Society*, 1885.

During four years I have seen three other bodies in which bifid ribs or cartilages were present. In two of these the left fourth cartilage and rib were affected, but of the third I have lost the notes, and only remember that one rib, or one rib and cartilage were affected. Professor Struthers, in his paper¹ in the *Jour. of Anat. and Phys.*, describes five cases of this condition. In three of these the abnormality was ascertained to be of the fourth rib, another probably of the fourth, the other two probably either of the fourth or fifth. In three it occurred on the left side only, in one on the right, in one on both sides.

I have also seen two subjects in which the costal cartilages were bifid, but the upper limb of the divided cartilage ended in a free rounded extremity, and did not, as in the previously described cases, include a foramen. The fourth costal cartilage was the one affected in both cases. In the first, which was a female subject, the manubrium was $2\frac{1}{4}$ inches long, and the gladiolus $3\frac{1}{2}$ inches. They articulated with one another by an amphiarthrodial joint. The right fourth costal cartilage was $\frac{5}{8}$ inch broad at its attachment to the sternum. At about

¹ "Variations of the Vertebrae and Ribs in Man," vol. ix.

half an inch from its inner extremity it split into two, the lower division taking on the functions of the normal fourth cartilage; the upper division, which was 1 inch long, ending in a free rounded extremity. The breadth of the fourth rib was increased abruptly at a point about 1 inch from its anterior extremity, showing a tendency to bifurcation of the rib also.

In the second case, which was a male subject, the manubrium was $1\frac{3}{4}$ inches long and the gladiolus about 4 inches. These bones articulated by an amphiarthrodial joint. The left fourth costal cartilage was more than $\frac{1}{2}$ inch deep at its inner extremity. It bifurcated in a similar manner to the last, the rib being, however, normal in form and outline. The free end of the upper division terminated abruptly in the intercostal muscles as in the preceding case.

Another point I would call attention to is the relative lengths of the clavicles on both sides. I find it stated in *Gray's Anatomy* that the right clavicle is frequently shorter than the left. I have measured a great many, and have not been able to verify this statement, either in people who had or who had not led laborious lives, nor do I see for what reason the right clavicle should be shorter than the left. Long before the clavicle would yield and alter its form under the influence of pressure, the first rib would have yielded to a relatively greater extent, and in it even a slight depression is rare. I have described fully the manner in which force is transmitted from the arm and shoulder to the chest wall in papers contained in the *Transactions of the Pathological Society*, 1884-1885, "Case of Costo-Chondral Dislocation," "One Mode of Fracture of the Sternum," and "Mode of Fracture of First Rib alone," so will not do more than refer to them here.

Whenever I have found the first costal arch equal on both sides, as is usually the case, the clavicles have also been symmetrical, but when the span of one arch was larger than its fellow, the clavicle on the same side was correspondingly so also. As a very marked instance of this, I would refer again to the cases already mentioned as having been described in the paper on "Supernumerary Cervico-Dorsal Bearing Ribs," in which the span of the costal arch on which the right clavicle rested was $3\frac{1}{4}$ inches, while that crossed by the left clavicle was only 3 inches. The right clavicle was 6 inches long, and the left $5\frac{1}{2}$ inches. This is a considerable and an unusual difference, but the difference between the costal spans was also great.

Returning to the case I was describing, the clavicles were equal in length. Their inner extremities were peculiar in that they were much flattened on their under surfaces, the articular surfaces on their inner aspect being continuous, with large flat facets on the under surface.

This last articulated with a correspondingly well marked depression on the upper surface of the first cartilage. The ligaments connecting the clavicles to the sternum and first costal cartilage were very well developed, and this was particularly the case with the interclavicular ligament, which was very thick and strong, and had hardly any connection with the sternal notch. There was no rheumatoid change in this or in any other articulation in the body. In the resting position, the clavicle lay on the first cartilage at a point half an inch internal to the attachment of the first rib, being much within the normal point of crossing. Also, on pressing back the shoulder, the clavicle could not be made to press on the rib where it received the insertion of the *scalerius medius*. This was due in part to the remarkable change in the form of the sterno-clavicular articulation, and in part to the shortness and great strength of the rhomboid ligament, and to the slight difference in the direction of the ossified cartilage.

On the left side the subclavius muscle was entirely absent, and the costo-coracoid membrane was ill developed. On the right side both were fairly well marked. In this case I did not see this part of the body till this region had been partly dissected, so cannot testify with absolute certainty to the complete absence of the left subclavius muscle. I was then unable to find any relic of it, and was quite satisfied that, if it had been present, it must have been very small indeed.

The coraco-humeral ligament on the right side was replaced by the tendon of the *pectoralis minor*. The left was normally attached. The right coraco-brachialis arose by a large fleshy belly from the whole length of the coracoid process as well as by the tendon common to it and the biceps.

I mention these abnormalities as I have frequently noticed that, when you get an abnormal condition of the thoracic wall, you not uncommonly get other parts varying also, especially structures about the clavicles and shoulders. I would refer again to a case I described in which there were thirteen cervico-dorsal vertebræ bearing ribs. In that there were on both sides chondro-epitrochlearis and three headed biceps muscles, besides several other muscular abnormalities. In the case which I have already referred to twice, in which there were apparently eight cervical vertebræ, the omohyoids had each only one fleshy belly, the anterior, and this arose by an aponeurosis from the clavicle. The subclavius muscle was also absent on both sides.

Simple costal and sternal asymmetry may be regarded as a condition of retrocession to the arrangement found normally in the orang-utans, and Professor Turner has demonstrated the fact that in Cetacea cervical ribs also exist not unfrequently, that they may fuse with the first thoracic rib, and that the upper two thoracic ribs may also unite, though not with the same frequency. Similar variations in the number of the ribs and in their degree of development have been described by Pro-

fessor Struthers among other animals. I have not succeeded in finding instances of bifid ribs or cartilages in any animal except man, but my experience is limited to museum specimens alone.

The next important point I will allude to is a very remarkable change in the outline of the shoulder-joint, and consists in an alteration in the relation of the head of the humerus to the acromion process. I need not do more than refer to the normal form of the shoulder as seen in people who do not lead very laborious lives. Its rounded shape is unbroken by any prominence of the acromion on its posterior aspect, or of the humeral head on its anterior aspect. The head of the humerus is sheltered by the acromion above, the small interval being filled in by the deltoid.

In some subjects, who have led hard laborious existences, I have found that the head of the humerus did not occupy the normal relative position to the acromion, and that the direction of the glenoid cavity was more anterior than usual. This modification in the form of the shoulder-joint does not appear to be limited to subjects whose spinal columns presented any particular labour curve.

The alteration consists in a forward displacement of the head of the humerus, so that it is no longer covered by the acromion to the same extent as before, and in the variation of the direction of the glenoid cavity from the normal, which I have just described. I was inclined to regard these changes as the product of strain thrown upon the articulation in certain employments.

The shoulder-joint of this subject displayed the above conditions in an extreme degree, so much so, that before the removal of the skin the appearance presented was that of double subcoracoid dislocation, in which a new socket had formed for the head of the humerus, and this socket had trenced considerably on the glenoid cavity. The anterior extremity of the acromion projected outwards behind the centre of the head of the bone, and the posterior part of the acromion projected back some way beyond the humeral head, so as to produce a considerable interval between these points. This was even more marked on the left side. The direction of the glenoid cavity was altered very distinctly.

The man was powerfully built, and his muscles were well developed, especially the deltoid and trapezius.

The question now arises as to the mode of origin of this condition. Is it the result of the occupation of the individual or of some fault in deportment, and produced in the same way as pressure changes elsewhere? In a subsequent paper¹ I hope to show that the shape of the head of the femur and the form and extent of the acetabular cavity is modified very considerably by the mode of labour of the individual, and that there can be no reasonable doubt in that case as to the manner of its production. In it the result produced by pressure is similar to that present in this shoulder-joint. I might also refer to changes in the direction of other joints as the result of pressure, which I have described in a paper in the last number of the *Guy's Hospital Reports*, "Senile Changes," &c.

Or is this condition of the shoulder-joint one that is peculiar to the individual and congenital, as are his bifid ribs, &c., and due to some cause of which we have no knowledge?

Though the vertebræ were strong and dense, this man's spinal column presented no pressure curve, except a slight forward curve of the upper dorsal vertebræ and an increase in the size of the lumbar and sacral spinous processes. His first ribs, as well as their ossified costal cartilages, were particularly strong. The sternal articulation was broad and firm. As I said before, the ligaments in connection with the clavicle were very strong, the interclavicular having but slight connection to the sternum. The clavicles also rested on the first cartilages and not on the ribs, and the line of direction of the cartilage and rib was altered from the normal.

Each of these circumstances taken separately does not prove much, but all taken together suggest strongly that the man had been engaged in some occupation in which he was in the habit of carrying heavy weights simultaneously in both hands, and that the conditions present resulted from the long-continued pursuit of this form of labour. Observing the different classes of labourers, one sees that there are but few whose function it is to

¹ "Pressure changes in the joints of the extremities, including senile changes," *Transactions of the Pathological Society*, vol. xxxvii., and "Dupuytren's contraction," &c., *Guy's Hospital Reports*, vol. xliii.

carry weights for any long time in this way, though of course many combine this largely with others. Perhaps milkmen more than others would seem to supply the necessary requisites for the conditions present in this skeleton.

*Fusion of the First and Second Costal Cartilages on the
Left Side.*

I am describing this specimen as it is a good instance of an unusual condition, and also because its characters will be seen to deviate slightly from those usually present in these cases, in regard to the span of the upper ribs, and the relative measurements of the manubrium and gladiolus. In a paper in the *Guy's Hospital Reports*, vol. xlii., "Cervical and Bicipital Ribs in Man," I gave descriptions of three instances of this form of abnormality, and the chests of these subjects were characterised by the relative diminution in the capacity of their upper part, including the manubrium, and by the relative increase in that of the lower part, including the gladiolus, and in the number of ribs articulating with that bone.

In the first case (fig. 6) the manubrium was $1\frac{3}{4}$ inches long, the gladiolus $4\frac{3}{8}$ inches, and eight cartilages articulated with the sternum on the side opposite to that on which fusion was present, namely, the left.

The cartilages articulated symmetrically with the sternum, except below, where the sternum itself deviated to the right. The first and second cartilages were fused through at least an inch of their extent.

In the second case (fig. 8) the right first and second costal cartilages were fused along $\frac{3}{8}$ -inch of their length.

The span of the first rib was $2\frac{3}{16}$ inch, the manubrium was under 2 inches, and the gladiolus over 4 inches.

On either side eight ribs articulated symmetrically with the sternum.

In the third case both first and second costal cartilages were fused in half an inch of their extent. The manubrium was $1\frac{1}{2}$ inches, and the gladiolus $4\frac{1}{2}$ inches long. There were on either side eight costal cartilages articulating asymmetrically with the sternum. As one would expect, the first and second alone of the upper costal cartilages ever unite.

This new specimen existed in the body of a well-built male subject with a good large chest.

The greatest span of the right first rib was $3\frac{3}{4}$ inches. That of the left was $3\frac{1}{2}$ inches.

The span of the right second rib was a third of an inch greater than that of the left.

The manubrium was $2\frac{1}{2}$ inches long, the gladiolus $4\frac{1}{2}$ inches.

There were seven ribs articulating symmetrically with the sternum.

The twelfth rib was 6 inches long.

The first and second right costal cartilages were normal in their form and arrangement. The first was ossified nearly throughout, and presented an arthrodial articulation in the normal situation.

The two upper left cartilages were fused in the inner inch of their extent, five-eighths of the first being free and half an inch of the second. The fused cartilage, as in fig. 6 referred to above, only articulated by a small surface with the gladiolus.

I would call attention to the extent to which this fused cartilage has undergone ossification. That part of it formed by the first costal cartilage was completely ossified, and presented an arthrodial joint at its outer extremity, that portion which was not fused articulating with the fused part. The line of ossified cartilage crossed obliquely downwards and inwards that part of the fused cartilage corresponding to the second costal cartilage, the *remainder of it being free from any osseous change*. There was no ossification of the other costal cartilages. Though the whole of the fused cartilage was subject to the same influence in respiration as was the first costal cartilage on the right side, yet, as we have seen, *only that portion of the fused cartilage corresponding to the first costal cartilage underwent any osseous change*, and the process of ossification was so far advanced as to necessitate the presence of a loose arthrodial articulation.

In previous papers¹ in the *Trans. Path. Soc.* I have described the mode of formation of this joint in the ossified cartilage, first in the sternum, and in the articulations connected with it, also the joint formation in the less frequently ossified lower cartilages. I ascribed the joint formation in the first cartilage as being due to two factors, the movements of respiration and the leverage action of the clavicle on the manubrium and first costal arch. I considered that the ossification of the first cartilages, *at a period long antecedent to that of the other cartilages*, was due almost entirely to the strain exerted on it by force transmitted through the clavicle. I then supposed that the leverage action of the clavicle and the movements of the sternum in respiration were the causes which determined the joint-formation in the ossified cartilage, and that of these two the former was the most important factor in its production.

I think the conditions presented by this fused first cartilage go far to prove the truth of that hypothesis. Against it, however, there is the fact that where other cartilages besides the

¹ "Case of Costo-chondral Dislocation," vol. xxxiv.; "Mode of Fracture of the Sternum," vol. xxxv.; "Mode of Fracture of First Rib alone," vol. xxxvi.

first ossify, they also develop an articulation. For further details I would refer to the papers already mentioned.

This man had been a labourer, and his spinal column showed extensive pressure changes.

Two Subjects with Six Lumbar Vertebrae, the First Lumbar Vertebra in one possessing Lumbar Ribs. Bifid Spinous Processes in Lower Dorsal Region. Separation of the First Piece of the Sacrum. Fusion of the Sacrum and First Lumbar, &c.

Before commencing the description of these cases, I will refer for the third time to the case in which there were thirteen cervico-dorsal vertebra bearing ribs,¹ besides seven cervical and five lumbar vertebrae. In that paper I entered into what now appears to me to have been rather a barren discussion, namely, as to whether the extra vertebra was a dorsal vertebra with ribs deficiently developed, or an eighth cervical with cervical ribs, and I then concluded in favour of the last supposition. The question would now appear to be a less obscure and a more general one.

There was one point I did not mention in that paper and which will bear on the question. It is one that must be of great obstetric interest. That is, that the oval facet on the upper surface of the sacrum occupied a lower position than usual, and that the line prolonging its direction forwards cut the symphysis just below its upper margin. The reason I did not describe this at that time was because I had not then succeeded in separating very distinctly the various modifications in form which the lower part of the spinal column undergoes under the influence of continued and exaggerated superjacent pressure, or of ordinary pressure acting on an enfeebled subject, and I then thought that the condition of the sacrum present in this subject was produced in a like manner, especially as there were marked pressure changes in the whole column. Thinking it had no bearing on the subject under discussion, I left it out of the paper.

Since that time I have been able to separate and classify the

¹ "Supernumerary Cervico-Dorsal Bearing Ribs," *Journal of Anat. and Phys.*, 1885.

pressure changes in the lower part of the spinal column, and I have described them fully in a paper¹ in the *Transactions of the Pathological Society*. I then found that the conditions presented by this sacrum were quite distinct from those produced by pressure, though resembling them superficially. I was also able to show in that paper that the larger number of the numerous modifications in form of the lumbar and sacral spinous processes, and in the form and direction of the articular processes, were due to pressure, and were not instances of congenital deviations from the normal, as supposed up to the present time by those who have observed them.

On examining other specimens, in which there were six lumbar vertebræ, I found the same condition of the sacrum present.

In the normal sacrum, if the direction of the plane of the oval articular surface be continued forwards, it will be seen to pass about an inch and a half above the symphysis, and the upper limit of the sacral body is found to be considerably above the level of the brim of the true pelvis.

With these facts before me, I examined the two following cases very thoroughly with the view of clearing up the difficulty.

The first subject was a well-formed male, above the average height. His bones were dense and strong, and he still retained most of his teeth.

The spinal column showed no marked pressure change. The lumbar convexity was very prominent, and much longer than usual.

The direction of the oval facet on the upper surface of the sacrum cut the symphysis immediately below its upper limit, and the facet was seen to be on the same level as the ileo-pectineal line, therefore considerably below its normal position.

As a result of this, the upper aperture of the true pelvis was heart-shaped, the apex of the heart corresponding to the back and of the symphysis, and being therefore flattened. The true pelvis was small, and its antero-posterior diameter at the inlet particularly so. I have unfortunately mislaid the measurements.

There were six lumbar vertebræ, the uppermost having on either side ribs one inch long, and articulating with either side of the body by a small facet with a synovial membrane, and posteriorly with the small transverse process. The transverse process of the third lumbar vertebra was longer than any of the others. The first lumbar nerve gave off the ilio-hypogastric and the ilio-inguinal, the second gave off

¹ "Pressure Changes in the Lower Part of the Spinal Column," vol xxxvi.

the genito-crural, and the obturator and anterior crural nerves came off from the second, third, and fourth lumbar nerves. The fifth lumbar passed down over the upper surface of the sacrum, and gave off the superior gluteal. The sixth lumbar nerve passed down to form part of the sacral plexus. The first sacral nerve joined with the two last. The second sacral nerve was small compared to the first, and was no larger than the normal third sacral. There was a very small third sacral, and it took the normal distribution of the fourth. The fourth resembled in distribution the normal fifth; it did not enter into the formation of the sacral plexus.

On making a vertical median section of the lumbar spine and sacrum, the latter bone was seen to consist of five parts, the limits of the bodies of the first three being still indicated by layers of fibrous tissue.

On comparing with this section another obtained from a normal column, it was then seen that the first piece of the sacrum had become separated so as to form the sixth lumbar vertebra, which the first coccygeal had united with the sacrum, so that it still consisted of five pieces. As we have already seen, the mode of distribution of the sixth lumbar was that of the normal first sacral.

On removing the fibro-cartilage between the sixth lumbar vertebra and sacrum, and then making these two bones articulate directly, the appearance given by the normal sacrum is obtained.

This shows that at least in this case and in similar ones an extra vertebra is not interposed between the occiput and attachment of the iliac bones to the spine, but that the first sacral vertebra, which does not seem to form a necessary part of the sacro-iliac articulation, is separated from the rest of the bones, the sacrum having joined to it the first coccygeal vertebra. Modifications in the form of the thorax are also present in these cases of dissociated first sacral vertebrae, and they consist in an increase in the size of the lower part of the chest, and a corresponding decrease in the capacity of the upper part. In this subject the manubrium was one and a half inches long. The span of the first rib was two and three-quarter inches. Eight cartilages articulated symmetrically with the sternum, and the twelfth ribs were more than 7 inches long. The costal cartilages were shorter than usual, but they were equal on both sides. The pleura extended for an inch and a half below the lower margin of the last rib.

The LOWER LIMIT OF THE PLEURA is a point that deserves much attention, especially now that the kidney is so frequently removed or explored from the loin, since opening of the pleural cavity at this point has caused both immediate and subsequent danger. This I have alluded to in describing the operation.¹ The lower limit of the cavity behind can be determined clinically by measuring the lower ribs, and especially the twelfth.

¹ "Nephrectomy:" *Manual of Operative Surgery*.

It will be found that if the twelfth ribs are under two inches in length, the pleura may not even reach its upper margin, or, at the most, it may extend but a little way over the inner half of its anterior surface.

As the length of this rib increases, the pleura extends still lower down, and in some instances, as in that just described, it may reach a point an inch and a half below the lower border of the rib.

If the last rib be over two inches in length, the lower limit of pleura *crosses it obliquely at its centre*, so that it bears a direct relation to the length of the rib. This relationship of the pleura to the length of the last rib shows that there need be no risk of opening this cavity in the ordinary operation of lumbar nephrectomy. In the description of the extent of the pleura in *Quain*, vol. ii., the following somewhat vague reference is made:—"Behind, the lower extent of the pleura is as far down as the vertebral end of the twelfth rib, or even in some cases as far as the transverse process of the first lumbar vertebra." The great and frequent variations in the length of the lower ribs, not always on both sides, and the consequent modifications in the form of the thorax, are not considered by anatomists in their description of the pleural limits. For instance, Luschka says that in the axillary line the right pleura extends down to the lower edge of the ninth rib, while the left pleura reaches to the upper edge of the tenth. In the many bodies I have examined for this purpose, I have been unable to verify this greater downwards extent of the pleura on the left side; in fact I have found the reverse more frequently true. Taking the average of a number of cases, the lower limit of the pleura crossed the seventh costal cartilage obliquely about three-quarters of an inch below its articulation with the rib, then the end of the eighth rib, or the cartilage immediately below it, the ninth rib a quarter of an inch above its extremity, the tenth rib three-quarters of an inch, and the eleventh one and a quarter inches from its outer end. In the axillary line, which is at least sometimes defined as a line passing vertically down from the head of the humerus, I found that in the large majority of cases the lower limit crossed the tenth space or the eleventh rib, not unfrequently lower on one side than on the other, but not much

more frequently on one side. Luschka probably used the term in a different acception, yet that fact would not modify the relative extent of the limit on both sides.

The second case, in which there were six lumbar vertebræ, resembled the last pretty closely. It was also a male subject. The lower part of the chest was relatively large and the upper part small. The sternum had been removed before the subject came into the room. The subclavius muscle was abnormal on both sides, the tendon splitting into two divisions, of which each had a muscular belly, one being attached to the upper margin of the scapula, and the other to the normal attachment of the muscle to the clavicle. The sacrum consisted of five pieces, but on making a vertical median section of the pelvis it was seen that the last piece was the first coccygeal, which had become fused to the sacrum. The pelvis presented the same changes as those described in the last case. It was small, considering that the man was much above the average in size and build. The upper aperture of the true pelvis was typically heart-shaped. Its antero-posterior diameter was only three and a half inches, while its greatest transverse diameter measured five and a quarter inches. In the average male pelvis these diameters are four inches and four and a half inches respectively, so in this case the *conjugate was considerably decreased*, while the *transverse diameter was increased*. The interval between the anterior superior spines was ten inches, the normal being seven and three-quarter to eight and three-quarter inches. The sacro-vertebral angle measured 130° , this angle averaging usually from 110° to 125° . The breadth of the sacrum was about normal, namely, four and a half inches.

The separated first sacral vertebra resembled the last lumbar in appearance, except that the right transverse process was very large and articulated with the surface of the ilium by an expanded flat facet. The left transverse process was longer than that of the normal fifth lumbar. The formation of the lumbar and sacral plexuses was identical with that described in the last case.

The lumbar curve was very prominent indeed, producing well marked lordosis, and consequent backward protrusion of the buttock and an increased obliquity of the position of the pelvis. This condition of sacral dissociation is probably the

reason of the lordosis and considerable gluteal prominence which one sees occasionally, and which dates back in these cases to early life. It may be very easily overlooked, as the superficial deviations from the normal are very slight indeed.

The spinous processes of the lower two dorsal vertebræ and the upper three lumbar vertebræ were very peculiar. The spine of the tenth dorsal vertebræ was very broad and expanded at its posterior extremity, where it presented a vertical groove in its centre. The spine of the eleventh dorsal was also very thick and strong. It was completely bifid at its extremity, the divisions also being thick and strong. That of the twelfth was similar in form, except that both the spine and its bifurcation was even stronger. The spine of the first lumbar vertebra was very thick, and terminated in a great flat end, measuring transversely three-quarters of an inch, and five-sixths of an inch in the vertical diameter. The spine of the second lumbar was similar in form and structure, and ended in a smaller plate than the last.

The spine of the third, fourth, fifth, and sixth were like those of the ordinary lumbar vertebra in form. They were very strong, but their depth was not exaggerated, so that they did not articulate directly with one another. On the lower margin of the second, third, and fourth lumbar spines there were on either side, at a point half an inch from the apex, large prominent nodules receiving the insertion of tendons of the multifidus spinæ.

Between the bifid extremities of the tenth, eleventh, and twelfth dorsal spines and the spines of the adjacent vertebræ there were pairs of interspinous muscles covered by a strong layer of supraspinous ligament. Between the spines of the first and second lumbar vertebræ there was a single layer of interspinous muscle, beneath a very dense supraspinous ligament, and between the spines of the lower lumbar vertebræ and the sacral spinous process there was an extremely thick and dense ligamentous tissue.

The erector spinæ and multifidus spinæ muscles in the lumbar region were remarkably large, and the aponeurosis covering them particularly strong and dense.

The reason of all this increase in the size of the spinous pro-

cesses, and in the bulk and strength of the ligaments and muscle, was to compensate for the great concavity and length of the lumbar region, and the consequent greater force required to raise the flexed upper part of the trunk upon the sacrum.

I have never before seen this splitting and enlargement of the lumbar and dorsal spines which were present in this specimen, nor have I read of it anywhere.

The necks of the thigh-bones joined the shaft at an extremely oblique angle. I mention this fact as I see that the same remarkable obliquity of the neck was present in a specimen of what appears to have been dissociated first sacral vertebra, which is described by Professor Struthers in page 83, "Variations of the Vertebrae and Ribs in Man."

This man also had a remarkably large head, whose increase in size was most marked in its antero-posterior diameter. The left side was the larger throughout. The increase in the transverse diameter and the decrease in the conjugate diameter of the brain are in a direction the reverse of retrocession to a lower type, as is also the increased capacity of the cranial cavity.

With this case we might compare an example of fusion of the sacrum with the fifth lumbar vertebra. This is distinctly a condition of retrocession, as the last lumbar vertebra not unfrequently joins with the sacrum in the gorilla, orang, and chimpanzee. It was a male subject, whose chest was of an average size, the manubrium and gladiolus having their average relative size. The last ribs were about 8 inches long, consequently there was but a narrow interval between it and the iliac crest. The margin of the fifth lumbar was united to the first sacral by bone, the intervening fibro-cartilage being much diminished in depth. The lumbar vertebrae formed with the sacrum an angle of 145° . The conjugate of the brain measured $4\frac{1}{4}$ inches, and the transverse diameter $8\frac{1}{4}$ inches. The neck of the femur joined the shaft at an angle slightly less than normal. This was not a very typical case of fusion of the sacral and last lumbar vertebrae, as the union of these two bones was not complete. After the bone connecting their margins had been cut through with the contained fibro-cartilage, the laminae and spinous processes were found to be quite free, the articular surfaces of the last lumbar vertebra looking directly forwards. Probably on this account the pelvis does not deviate very markedly from the normal.

NOTE ON A CASE OF BICIPITAL RIB. By R. L. MAC-DONNEIL, M.D., *Demonstrator of Anatomy in McGill University, Montreal.*

THE recent article of Professor Turner on "Cervical Ribs and the so-called Bicipital Ribs in Man," in the *Journal of Anatomy and Physiology*, vol. xvii., as well as his previous contribution on the subject of the so-called two-headed ribs in whales and in man, vol. v., leaves very little to be said upon the subject of fused ribs; but inasmuch as the occurrence of this abnormality is rare, it may be well to place upon record a description of a case of bicipital rib which came under my notice in the dissecting-room of McGill University in the winter session of 1884-85.

In a male subject the first and second ribs on the right side were joined up to a distance of an inch from their cartilages. The first rib has a normal head articulating in the usual manner with the first dorsal vertebra. The neck of the rib is rather more bent upon the shaft than is usually the case, and its width from before backwards, at the tubercle is beyond the normal. The junction with the second rib takes place at a distance of five-eighths of an inch from the tip of its tubercle, the fusion being apparently from above downwards, as if the ribs were laid one on the top of another. For a little more than one-half the distance between the tubercle and the sternal extremity, the first rib in outline is distinct from the second, there being a shallow groove between the two bones, but after this point the junction of the two ribs takes place more by their borders than by their surfaces, so that they form a large flat plate of bone gradually spreading out to a maximum width of two inches. On holding the specimen up to the light the two ribs are seen to be separated from one another by a very thin transparent plate of bone for a distance of half an inch from their point of fusion. On the outer surface of the fused body there is the usual rough surface on the second rib for the attachment of the serratus magnus muscle. The rough line commonly seen on the upper surface of the first rib,

which gives attachment to the scalenus medius is not distinctly marked upon the first rib, but is plainly seen extending from its usual site over that portion of the fused body which belongs to the second rib. The scalene tubercle is not distinct. The bifurcation takes place anteriorly, at a distance of 3 inches from the tubercle of the first rib. The upper branch of it ends abruptly in the cartilage of the first rib, while the lower branch, the continuation of the second rib, is one and a half inches long, three-quarters of an inch wide at its outer, and one-third of an inch wide at its sternal end. The costal cartilage to which this lower branch is attached ends in the usual position of the second costal cartilage.

On the under surface the fused body presents a smooth surface for the protection of the upper part of the pleural cavity.

Owing to an unfortunate occurrence,—the removal of the ribs soon after their peculiarity had been observed,—I am unable to give any account of the dissection of the soft parts.

In this same subject it was found on cleaning the skeleton that the first dorsal vertebra presented a remarkable abnormality. The laminæ of the neural arches of each side do not run on the same plane, the one with the other; but one, that of the left side, is higher than that of the right, so that the spine of the vertebra is formed by the placing of one lamina over the other.

OSTEOLOGY OF CONURUS CAROLINENSIS. By R. W.
SHUFELDT, M.D., *Medical Corps U.S. Army; Membr. A.O.U.;*
Membr. Soc. Nat. E.U.S.; Membr. Philosoph. Biol. Socs. of
Washington, &c. (PLATES X., XI.)

WE learn from the best authorities on the subject, and those who have given special attention to the *Psittaci*, that we may reckon something over three hundred and fifty well determined species of Parrots in the world's fauna, so far as it is at present known. The strongly marked characters and the unmistakable external appearance of any of the forms that go to make up this wonderfully interesting group of birds, have long served to clearly distinguish them from other, and perhaps not so well defined, orders of the class. Fortunate as ornithologists have been in this respect, the matter of drawing the lines for the minor divisions used in classification has, since the earliest days of the science, owing to the perplexing interrelation of the majority of the forms, proved a far more difficult task. The several schemes proposing as many arrangements into families were all more or less unsatisfactory, until the subject came under the master-hand of Garrod, who, through his able and well-directed investigations into the structure of the leading types of the order, showed how the entire group could first be divided into two primary series, viz., the PALÆORNITHIDÆ, and the PSITTACIDÆ.¹ The former of these (excepting *Cacatua*) having two carotids, the left one being normal, and no ambiens muscle; while, on the other hand, the remaining series have the two carotids present, the left one being superficial, and the ambiens, present in some of its genera, is found to be missing in others.

Fourth among the divisions of the second series, or in the *Psittacidæ*, we find the *Arinæ*, characterised by the presence of the ambiens muscle, tufted oil-gland, and union of the clavicles at their lowest and median point, into a complete os furculum.

¹ Garrod, A. H., "On some Points in the Anatomy of the Parrots, which bear on the Classification of the Sub-order," (*P. B. S.*, 1874, pp. 586-98).

To this sub-family *Arinæ* belongs the sole representative of the Order in the avifauna of the United States, the Carolina parrot, and it is to the description of the skeleton of this form that the present memoir is devoted.

Formerly the geographical distribution of this bird spread over a much larger area, but of late years, between the interests of feather-dealers, and its general wanton destruction, the complete extermination of the species seems to be as certain as it is no less a much to be regretted fact.

My first attempts to secure a skeleton of this bird, for the purpose of description, failed, and it was not until Mr James Bell of Gainesville, Florida, cheerfully came to my assistance that success at last was met. This gentleman, always ready with his aid in the interests of science, forwarded me two very complete skeletons, a male and a female of this species, to meet the end I had in view.

This very acceptable gift came to my hands in March 1885, at a time when every moment of my spare hours was being devoted to a large mass of material, chiefly osteological, illustrating the American sub-polar avifauna, and belonging to the Smithsonian Institution, so that it was not possible until the present month, August 1885, when my labours in that direction ceased, that I could at last give my attention to placing on record an account of the skeleton of our little Carolina parroquet.

Of the two skeletons in question, I chose the male to make my drawings from in the plates, and I found it to be somewhat larger than the female specimen. Notwithstanding, both were evidently adults.

Of the Skull (Pl. X. figs. 1-4).—In *Conurus* the culmen of the superior mandible or its middle line lies in the arc of a circle extending from the cranio-facial axis to the tip of this part of the beak. Posterior to the subcircular osseous nares this culmenar surface is broad and nearly flat, but beyond these apertures it is convex, both transversely, and as has been said, along its middle line. The dentary margins of this mandible are cultrate and deeply notched at their middle points, as shown in figure 1, where the skull is represented upon lateral aspect.

Complete absorption of the nasal bones has taken place, so

that in the adult their existence would never be suspected, and their exact limits can only be guessed at, as no sutural traces remain.

The under side of this mandible is bounded behind by a straight, transverse line, beneath which the palatines are inserted. Its general surface, otherwise, is unbroken, and evenly concave throughout (fig. 4).

The interior of this part of the skull is more or less filled up with an osseous, spongy tissue, that presents a more compact nature where it forms the anterior wall to the rhinal chamber. One cannot very well judge as to how much, if any, of this structure can be claimed as representing the maxillo-palatines in this parrot.

Speaking in general terms, Professor Huxley says of the *Psittaci* that "the maxillo-palatines are very large and spongy in texture, and unite with one another and with the ossified nasal septum so as to fill up almost the whole base of the beak. Above, however, a nasal passage is left on each side; and, below the maxillo-palatines stop short, so that, in the dry skull, a passage, leading into the cavity of the rostrum, is left on each side of the septum."¹

These remarks are illustrated by the under view of the skull of *Cacatua galerita*, which bird, I think, from the drawing, must have its nasal septum as well as this spongy mass which surrounds, produced much further backwards than it is in the subject we have in hand. However, the parts no doubt are homologous in both of these forms, though one would hardly have suspected the mass in question to have represented a part of the skull deserving of a special name, had the Carolina parrot been the only bird examined.

Among the points that have always attracted the most attention in the skeleton of the *Psittaci*, the cranio-facial hinge is here in *Conurus* as perfect in its mechanism as we perhaps will find it in any of the order.

Its structure is too well known to enter upon its details here; I find, however, that neither in this parrot nor any other of the group that I have ever examined is this feature one whit better developed than it is in *Sula bassana*.

¹ Huxley, T. H., "On the Classification of Birds," *P. Z. S.*, 1867, p. 442.
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Passing now to other parts, we find the union between the sphenotic process and the descending portion of the lachrymal bone to be complete, forming an external orbital periphery or ring, which is very nearly circular (figs. 1, 4, *or.*).

According to Parker, this is through the intervention of the *os uncinatum*, which in some parrots, by union with the zygomatic process of the squamosal, bridges over the temporal fossa.¹

The lachrymal itself has indistinguishably, so far as a suture is concerned, merged above with the frontal bone, while its union with the sphenotic process, just alluded to, is equally well obliterated.

Internally it unites in a similar manner with the small *pars plana*, a circular foramen for the olfactory nerve passing between it and the ethmoid, while externally the antero-inferior arc of the orbital ring is marked by a longitudinal concave notch.

As for the orbital cavity itself, its walls are but fairly entire, the *pars plana* being small, and the exit from the brain-case for the first nerve being far larger than this branch demands. Moreover, the palatines being vertical plates in this situation, and the pterygoids slender, the floor of the cavity is necessarily badly provided for in this regard.

In both these specimens the foramina for the exit of the optic and the third, fourth, and sixth nerves are distinct, and scarcely any greater in size than the structures they are designed to transmit are in calibre.

The interorbital system is without vacuities, and directly throughout merges with the rostrum of the sphenoid beneath it, the lower margin of the whole plate being sharp, both inferiorly and in front.

Anteriorly the ethmoid bone proper is very broad, being spread out as an abutment against, and bordering for all its width, the posterior line of the cranio-facial hinge. The body of the bone is thickened and filled in with diploic tissue.

That portion of the skull which lies behind and below the orbital ring presents for examination, above the lateral aspect of the evenly-convex vault of the cranium, and below, the long

¹ Parker, W. K., *Morphology of the Skull*, p. 264.

squamosal process separated from the sphenotic by a well-defined valley.

The bony ear conch is circumscribed by sharp margins, while to its under side a vertical plate is thrown down the temporal wing of the exoccipital.

As is well known, the characteristic feature of a parrot's quadrate bone is, that its mandibular facet is single, and placed in such a way that its long axis is in the same straight line with the longitudinal axis of the pterygoid; to the possession of this narrow, convex, and long facet *Conurus* forms no exception. Above it, the body of the quadrate is flattened from side to side, with a conical projection on its outer aspect, posterior to its middle point, that has a pit as its apex to accommodate the apophysis on the inner side of the hinder extremity of the quadrato-jugal.

The orbital process of the quadrate is spiculaform and well developed, while the mastoidal limb of the bone rises as a stout subcylindrical rod, with two convex articular facets at its summit. These are divided by a notch, and the inner one of the two is very small, not presenting more than one-tenth of the amount of articular surface the outer one does. The pneumatic foramen is found near its most usual place, on the inner and back part of the mastoidal shaft.

Viewing the skull now from above as shown in fig. 3, we observe that the narial apertures can also be seen upon this aspect surrounded above by a few minute vascular foramina.

The cranio-facial hinge bordering the superior mandible behind, is found to be a transverse and depressed line extending all the way across.

Between the superior orbital peripheries the frontal region of the skull is smooth and nearly flat; as we proceed backwards it gradually becomes convex, to form the beautifully rounded vault of the cranium.

A few perforating foramina are found just within the two edges of the orbits in the frontal bones.

Turning to the under side of the skull (fig. 4), the most remarkable feature that confronts us is the extraordinarily fashioned palatines. These bones, as they occur in the *Psittaci*, have been described by a number of anatomists, so their peculiar conformation is well known. *Conurus*, like most true

parrots, has either of these bones horizontally flattened in front, where it is inserted above the hinder portion of the superior mandible to meet the lower part of the nasal septum, but not the palatine of the opposite side.

Proceeding backwards from this horizontal extremity, the palatine is seen to contract, then immediately afterwards to form a broad, oblong, and vertical plate. This plate has a certain limited portion of its antero-superior part curled towards the median line, where it meets a corresponding edge of the fellow of the opposite side; and the two here form, by the assistance of the palato-ptyergoidal articulation, the usual longitudinal groove for the under edge of the rostrum.

Behind this the superior margin of the palatine plate is sharp, and has the anterior two-thirds of the corresponding pterygoid resting upon it; the posterior margin shows a deep notch, while the inferior margin of this part of the bone is rounded, becoming in front continuous with the dilated anterior end.

Both the internal and external surfaces of these palatine plates may develop processes and ridges for the better insertion of muscles, which in life are thereto attached. A broad, spindle-shaped vacuity exists between these palatines in front, while posteriorly the angle separating their plates is somewhat less than the angle of divergence of the pterygoid bones (fig. 4).

These latter elements are long, nearly straight and cylindrical rods articulating as shown in the figures in the Plate (*pt.*). They are at some distance below the basis cranii; and in no parrot, so far as is at present known, do they develop basipterygoid processes.

The maxillary portion of either of the infraorbital bars (*mx.*) is inserted by a somewhat horizontally-flattened end, just within the posterior edge of the beak, on a higher plane than the insertion of the palatines, and at a point where I take the foot of the nasal to be. The remainder of the bar almost immediately becomes of a uniform calibre, and at first being concave outwards, passes just beneath the orbital wing, directly downwards and backwards to its articulation with the quadrate (fig. 4, *mx., ju.*).

At the cranial base we find a basitemporal area of small

extent, triangular in outline, bounded on all its sides by raised lines, and having its apex directed anteriorly, terminating at the point where occurs the naked and external double-tubed entrance of the Eustachian canals.

On either side of these apertures are seen from three to four, or sometimes only two, minute foramina. Well to the outer sides of these are the conspicuous foramina ovalia.

As has already been said in a former paragraph, the temporal wings of the exoccipitals are very prominently produced; and, as usual, to their inner sides at the basal angles of the basitemporal triangle are found the ordinary group of foramina for the entrance and exit of vessels and nerves.

The foramen magnum is of a subcircular outline, and the plane of its periphery makes an angle of some 20° with the backwardly-produced plane of the basis cranii. The condyle is comparatively large, hemispherical in form, and sessile.

Rising almost perpendicular to the basitemporal triangular, the occipital area is well defined by an elliptical bounding arc, which sweeps round on either hand to the apices of the temporal wings. In the middle of this space a moderately prominent, unpierced, supraoccipital elevation is to be seen. In removing the cranial vault I find that the tables are very closely juxtaposed, and, of a consequence, but a little diploic tissue present. The several cerebral fossæ are sharply defined by out-jutting lamelliform ledges of bone.

At the base of the sella turcica there seems to be but one carotid opening, and the posterior clinoid wall to this fossa is very thin, and usually exhibits one or two perforations.

The *mandible* (figs. 1 and 2) of *Conurus* is somewhat horse-shoe shaped, with very deep and smooth ramal sides, which are deficient anteriorly, leaving a semicircular opening with cutting edge all round. When the horny mandibular sheath is carefully removed in the fresh specimen, this edge has filiform prolongations of soft tissue standing out from its middle third below, which, after they have dried and become more or less shrunk, look something like a row of delicate teeth.

The ramal sides of this bone slope away as we proceed backwards, and the mandibular ends are truncated at about the same angle.

To the inner sides of these articular ends a ledge is thrown out to support the facet for either quadrate. Behind these longitudinal articular grooves single pits are found, at the bases of which the pneumatic foramina occur.

The under borders of the mandible are smooth and rounded (fig. 2).

Of the Hyoid Arches (Pl. X. fig. 5).—Notwithstanding the fact that the glossohyal which supports the thick, short, and fleshy tongue of this parrot remains in cartilage throughout life, the ceratohyals (*ch.*) are very completely developed, meet in the median line, and ossify up to the very hinder body of this element anterior to them. Where they unite at the mesial point behind, an articular surface is formed for the first basibranchial (*bh.*). This last-named element is unusually long, and anchyloses with the second basibranchial (*b.bh.*), the point of mergence being enlarged to accommodate the heads of ceratobranchials (*c.br.*), and anteriorly to support a peculiar osseous outgrowth (*bf.*), that, so far as I am at present informed, is restricted to the *Psittaci*; indeed, this is the only form in which I have observed this latter feature.

The ceratobranchials (*c.br.*) are very long, subcylindrical, and rather stout rods of bone; while, on the other hand, the epibranchials (*e.br.*) are notably short and but feebly developed. As thus constituted, the thyrohyal elements show but little curvature along their continuities, and still less disposition to curl up behind the cranium.

Of the Remainder of the Axial Skeleton (Pl. XI. figs. 8, 9, 10, 13, 15, 17, and 18).—*Conurus carolinensis* has thirty-five vertebræ in its spinal column, and a large pygostyle at its terminal extremity.

The *atlas* is characterised by a broad neural arch above, an unperforated cup for the occipital condyle, and a prominent process extending backwards from the pseudo-centrum behind.

Axis vertebra has a very inconspicuous odontoid process, strongly developed neural and hypapophysial spines, and tuberos postzygapophyses. This segment, like the rest of the column and the pelvis, is pneumatic; to this statement, however, the last five caudal vertebræ and pygostyle prove an exception.

Both third and fourth vertebræ have strong hypapophysial spines, and neural ones scarcely less marked. In these, too, the lateral canal are seen, but the processes at their hinder margins are, as yet, but feebly produced. The zygapophysial arms are short, and their being joined from before backwards in each case by bone extension lend to these two segments a width upon their dorsal aspects and a solid appearance not possessed by any of the other vertebræ below.

In the fifth vertebra the dorsal and ventral spines have lost not a little of their prominence, while the parapophyses are much longer. This segment has the postzygapophyses manifestly lengthened, whereas but little change has taken place in the anterior pair.

The sixth vertebra loses the neural and hypapophysial spines altogether; the parapophyses gradually diminish in size from this segment down the chain, until they, with the pleurapophyses, again become prominent as free ribs. Likewise the neural and lateral canals, which are here quite small, also increase in calibre as we proceed in the same direction.

This vertebra has also a short carotid canal present in place of the hypapophysis.

And this last feature is still better marked in the seventh vertebra, though it remains open below. These are the only two which have it in this parrot, in the eighth its site being again occupied by a low, median hypapophysial spine.

In all these segments, as well as in the few succeeding ones that we find before coming to the true dorsals, the pre- and postzygapophyses are diverging limbs of the most usual form in aves. The articulations among the centra are heteroccelous.

Ninth vertebra has the neural spine commencing to make its appearance again, and is here a low tubercle, more prominent in the tenth, and thus on till it assumes the dorsal form of this spine. The hypapophysial plates in both the ninth and tenth vertebræ are deep, long, and of a quadrate form, and from the lateral masses being low on the sides of the centra, they appear sunken between these protuberances.

We find that the twelfth vertebra has much the general aspect of one of the dorsals, and moreover, its pleurapophyses have become freed as a tiny pair of ribs. These attain quite

a respectable length in the thirteenth vertebræ, while in the fourteenth, where they are still unconnected with the sternum, they possess small unciform processes.

We may term the fifteenth to the eighteenth vertebræ inclusive true dorsals, for they all have ribs connecting them in the usual way with the sternum. They also have interlocking neural spines, and their transverse processes are strengthened by each one developing a single spiculaform interlacing metapophysis at its outer extremity. Prominent hypapophyses are found upon the thirteenth, fourteenth, fifteenth, and sixteenth, and a small one sometimes on the seventeenth vertebra.

The ribs have broad unciform processes anchylosed to them, but there are still two other pairs that come from beneath the pelvis, belonging as they do to the sacrum, that also meet costal ribs below, which do not have these appendages.

Sometimes abortive ribs are found anchylosed to the twenty-first and twenty-second vertebræ, these being the third and fourth segments appropriated by the sacrum.

Now, in my male specimen of this parroquet, I find the nineteenth to the twenty-ninth vertebræ, inclusive, form the pelvic sacrum, while in the female an additional segment, which in the male remains a free caudal, has become firmly attached behind.

This circumstance gives the male six free tail vertebræ, whereas the other specimen has but five. Such a freak as this, however, not unfrequently happens among birds, where the count for the entire number of vertebræ in the column remains wonderfully constant for the species.

The caudal vertebræ (fig. 13) have spreading transverse processes, and stumpy neural spines; the ultimate two having strong bifid hypapophyses.

Of an irregular quadrilateral outline, the pygostyle has thickened hinder and lower margins, while the remaining two are oculate.

Giving our attention now to the *pelvis*, we find this compound bone in *Conurus* (figs. 9, 10) devoid of any very striking features, it having all the general characteristics of this part of the avian skeleton, without any to particularly distinguish it beyond the general facies of its kind.

Viewed from above, it will be seen that the pre- and postacetabular areas are about equal in extent, the ilium being concave where it forms the first, and the reverse where it constitutes the latter. For the entire length of the sacrum these bones are firmly sealed to its outer margins, forming the most complete "ilio-neural canals" anteriorly, which do not even open posteriorly as in some birds; while behind it lends to the postacetabular area a very unbroken aspect, that is rendered even more so from the absence of all but a few small foramina among the sacral diapophyses.

Upon the lateral aspect of the pelvis we note that the propubis is not developed, and that the inner periphery of the cotyloid ring is nearly as large as the outer one. The small obturator foramen is rendered complete by a pretty thorough meeting between the ischium and the somewhat slender postpubis immediately behind it.

The obturator space is long and spindle-shaped, but the lower angle of the ischium does not need the postpubic shaft beneath it, as it does in so many birds.

The antitrochanter and the elliptical ischial foramen are both of comparatively moderate size, and these several features, constituting as they do a group of notable occurrence on the lateral aspect in nearly all avian pelves, are here in harmony, both as to size and position, with the same as they are found in the class's majority.

On the under side we find that the lateral processes of the leading four sacral vertebræ are thrown out as abutments against the nether sides of the ilia; beyond, or rather behind these, the usual cavity of the pelvic basin occurs, and the succeeding diapophyses of these consolidated vertebræ are less manifest than common, being all elevated and having their extremities in the roof above.

The foramina for the exit of the sacral nerves are double, in each case one being placed above another, and the swell to accommodate the myelonic enlargement in this part of the cord's track is here well pronounced.

Conurus, in common with many other parrots, has for its general size comparatively a large *sternum* (figs. 8 and 18). Seen from above we observe that the costal processes are but

scarcely produced above the lateral borders, which latter rise gradually to their summits. These costal borders each support six facets for the hæmapophyses, the concavities among them being pierced by small groups of pneumatic foramina.

The space occupied by one of these costal borders is equal to about half the whole length of the lateral sternal margin.

Posterior to them, on either side, the margins are sharp all the way round the xiphoidal extremity, this part of the bone having a shield-shaped outline, being concave above, though not nearly so much so as that part of the sternal body lying between the costal borders in front.

In this latter section we sometimes find a few scattered pneumatic foramina down the median line; the most constant, and a large one of these, however, is close up to the anterior border of the bone, which curls backwards over it, and the fossa thus formed is always spanned over by a median longitudinal bridge of bone.

The anterior sternal body is thickened, and directly over its sharpened edge in front we find a continuous coracoidal groove; beyond this there rears directly up a broad quadrate manubrium, which is continuous with, and has its lateral surfaces in the same plane with, the carina below.

Extending the entire length of the body of the bone the keel of this sternum is comparatively a very deep one. Both its lower and anterior borders are convex, the latter being quite sharp. The carinal angle formed by the meeting of these edges is rounded off, so that the lines form really one common curved line (fig. 8).

That anterior vertical and thickened column of bone which is present in the keel of nearly all avian sterna is here well developed, but situated at some little distance back from the anterior margin. Moreover, it does not descend so far as is usually seen, being apparently interrupted by the muscular line which longitudinally marks the bone.

The muscular lines of the pectoral aspect are roughly parallel to the costal borders, and remain quite distinct as we proceed towards the xiphoidal extremity, nearly as far as the elliptical fenestra that there occur, one on either side.

In the *shoulder-girdle* (figs. 15 and 17) we find a *scapula* with

rather a short blade though a stout one, having the usual sabre-like form with obliquely truncated extremity posteriorly.

It contributes the usual amount of articular surface to the glenoid cavity (*g.*), but when *in situ* does not occupy the entire length of the superior line of the scapular process of the coracoid, nor have any connection with the furculum except through a slight ligamentous attachment.

I have represented in the Plate the right *coracoid* (*c.*, fig. 17) as seen from a posterior view.

It will be at once observed that in *Conurus* this element of the girdle has a form that partakes much of the pattern it assumes among birds generally.

Its tuberosus summit is inclined slightly forwards and towards the median line, when articulated *in situ*, and has resting against it the frail clavicular head of that side. The scapular process already alluded to is well developed, but here chiefly given over to quite extensive ligamentous attachment.

The coracoidal shaft is strong, comparatively of good length, and subcompressed in the antero-posterior direction, being faintly marked at the usual sites by muscular lines.

At the sternal extremity of the bone we find the expanded portion, the form of which can best be seen in fig. 17, where we note that the lateral process at its externo-inferior angle is well marked.

Many parrots are notorious for having incomplete furcula, in others the union at their medio-inferior points is very feeble.

In this particular they resemble the *Strigidae*, a group they undoubtedly have some remote affinity with, in structure. Our Carolina parroquet has a complete *os furculum*, as shown in fig. 17 (*cl.*); it is, however, a very weak bone, and functionally accomplishes little more than an ossified ligament in the same position. Indeed, it reminds one very much of such a structure, for when duly articulated it is but little in advance of the imaginary plane that is tangent to the anterior surfaces of the coracoidal shafts, and consequently but little dissociated from the ligaments that descend from the coracoidal summits to meet for attachment on the top of the sternal manubrium. It is in form of the U-shaped pattern, and without a hypocleidium at the clavicular junction below.

As already intimated above, and so far as the light I have on

the subject will at present permit me to judge, I believe that the shoulder-girdle of *Conurus* more nearly resembles these parts in some of the owls than it does the corresponding lines in any other class of birds with which I am acquainted.

Of the Appendicular Skeleton (Plates X., XI., figs. 6, 7, 11, 12, 13, and 16).—A glance at the drawing in the Plate of the pectoral limb of this parrot will be sufficient to convince us that it presents no very striking deviations from the average skeleton of the wing as found in existing birds.

The bones are all harmoniously balanced both as regards their relative lengths and calibres.

Pneumaticity is enjoyed by the *humerus* alone (*h.*), and this bone is here characterised by a short, though not inconspicuous, radial crest, an ulnar crest devoted, as usual, to forming a canopy over the pneumatic fossa, in which are found the air-holes leading to the interior of the humeral shaft. This latter is but little curved in any direction, being subcylindrical and smooth. At the distal extremity of the bone we find the trochleæ for articulation with the antibrachial elements prominently produced, while on the obverse aspect a broad and a narrow gutter are seen, which guide the passing tendons in life.

The *radius* is nearly straight for its entire length, differing from the *ulna* in this particular, it having a considerable curve along its shaft, the concavity of which is on the radial side, and gives rise to quite a wide interosseous space.

This curvature of the *ulna* is not well seen in the drawing, because the bone is rotated there to a position that brings it on the side towards the observer, and consequently makes the shaft appear nearly straight.

The carpal elements (*re., uc.*) are two in number as usual, and they have the form most commonly presented by these bones throughout the majority of the class.

In the manus we find a carpo-metacarpus of the ordinary form for birds generally. Its rather large pollex phalanx is without a claw, this feature being likewise absent from the tip of the distal digit.

My drawing presents all these bones of the size they attain in an adult male parrot, with every important detail brought out, and held in such a position that their greatest lengths are

represented, and can be easily measured and appreciated from the Plate itself.

None of the bones of the pelvic extremity in *Conurus* have air admitted to their interiors, and they all become dark and greasy in the ordinarily prepared skeleton.

The *femur* has a large, semiglobular head, with a shallow, though quite extensive excavation upon it, for the round ligament. A broad articular surface is found at the summit of the bone for the antitrochanter of the pelvis, and the suppressed trochanterian ridge does not rise above this.

The shaft of the bone is but little bent in any direction, and it has the usual cylindrical form. At the distal extremity the condyles are fairly well developed, not strikingly large, the outer one being the lower when the bone is held in the vertical position. In front the rotular channel does not extend upon the shaft above them, while behind the popliteal depression is shallow also.

The cleft for the fibular head marks the posterior aspect of the external condyle, dividing it, as usual, into two parts.

Our subject possesses a small *patella* of a subcordate form, maintaining its usual relations with the bones of the leg and thigh (fig. 12, *P.*).

Tibio-tarsus (fig. 12, *Tt.*) has its cnemial crest but very slightly produced above the articulating surface at the summit of the bone, while below it the pro- and ectocnemial ridges are but feebly manifested, and very soon merge into the shaft.

This latter is quite straight and smooth, being slightly compressed in the antero-posterior direction.

At the distal extremity the inner condylar protuberance is decidedly the more prominent, both upon front and rear aspects. The valley between these two eminences is quite wide and well defined, even to the posterior side of the bone.

The osseous bridge for the extensor tendons is present.

Marked feebleness in development is displayed on the part of the *fibula* of the Carolina parrot, for this bone is found not to extend below the ridge it articulates with on the side of the shaft of the greater leg-bone. Below this point the inferior apex of the fibular shaft is produced and replaced by a ligament of hair-like dimensions.

What there is of the fibula in this bird, however, is fully as well developed as we usually find it in the class; simply its apparently useless prolongation, as seen in many birds, has never ossified.

In the skeleton of the foot we find a short, thick-set tarso-metatarsus, with spreading trochlear extremity. Three views are presented in the Plate of this bone, besides the one where it is shown on a lateral view with the foot as a whole (figs. 13 and 16).

Its shaft is short and straight, being much compressed from before backwards. On the anterior aspect it is convex from side to side, while behind it is longitudinally excavated. The hypotarsus is a narrow, projecting ledge with one vertical, cylindrical perforation (fig. 13, *st.*) near its centre, and scarcely grooved for the other tendons behind. At the summit of this bone we note the two condylar depressions for the trochleæ of the tibio-tarsus.

The usual arterial foramen pierces the shaft at its ordinary site at the distal end.

As is well known, *Psittaci* are permanently zygodactyle birds by reversion of the fourth toe, while they not only possess a well developed and free accessory metatarsal, but the usual number of joints to the digits. *Conurus carolinensis* agrees in all these particulars.

Whenever I can I make it a rule to fully illustrate in the figures the tibio-tarsus and skeleton of the pes, as the points presented by these parts stand among the most important in this all-important system of the bird's anatomy, for when sufficient data of this kind become available they will be not only valuable as an aid in classification, but help to determine the affinities of existing birds with such fossil forms as may from time to time be discovered. It will be seen that I have not overlooked this fact in the present instance.

Synopsis of the Skeletal Characters of Conurus carolinensis.

1. Superior mandible arched as in *Raptores*; osseous nares small, subcircular, separated by nasal septum. Dentary margins of mandible cultrate, and notched.

2. Orbital ring complete.
3. Cranio-facial hinge as in other *Psittaci*.
4. Lower margin of rostrum cultrate.
5. Quadrate has a large and small facet on mastoidal head, a well-developed orbital process, and a single, longitudinal mandibular facet, which is laterally compressed and convex in both directions.
6. Pterygoids long and slender rods, anteriorly articulating with each other and with the palatines.
7. Major portion of either palatine—a large vertical plate, directed downwards and backwards. These bones curl towards each other and form a limited articulation in the median line; anteriorly they are horizontally flattened, and are hinged to the mandible beneath the spongy mass, which constitutes the maxillo-palatine and nasal septum.
8. Mandible truncated in front; rami and symphysis deep and gradually round into each other.
9. Hyoid apparatus with large, united ceratohyals, and a peculiar bony outgrowth on either side of the first basibranchial, extending forwards.
10. Manubrium of sternum erect, large, and continuous with the deep carina. Xiphoidal extremity of this bone has an elliptical fenestra on either side. Costal processes low, and usually six hæmapophysial facets on each costal border. Coracoidal grooves unite in front.
11. Furculum of shoulder-girdle firmly united below.
12. The humerus only is pneumatic in the pectoral limb.
13. A well-developed patella present. Fibula short, extending only so far as the lower end of fibular ridge of tibio-tarsus.
14. The tendinal bridge at antero-distal end of tibio-tarsus at right angles to long axis of shaft. The inner condyle the larger and more elevated.
15. General skeletal characters of pes agree with other *Psittaci*.

Negative Characters.

1. Vomer absent.
2. Basipterygoid processes not developed.

3. No hypocleidium on os furculum, and this bone does not meet the scapular process of coracoid.

4. Propubis of pelvis absent.

5. Pelvic limb non-pneumatic.

DESCRIPTION OF PLATES X, XI.

Reference Letters.

b.	Basal view of left tarso-metatarsus.	ju.	Jugal.
bf.	Bony outgrowth from basi-branchial.	m', m''.	Middle metacarpal and its phalanx.
b.bh.	Second basibranchial of hyoid apparatus.	mx.	Maxillary.
bh.	First basibranchial.	or.	Orbital ring.
c.	Coracoid.	P.	Patella.
c.br.	Ceratobranchial of hyoid apparatus.	p.	Pollex phalanx.
ch.	Ceratohyals.	pl.	Palatine.
cl.	Os furculum.	pt.	Pterygoid.
c.br.	Epibranchial of hyoid apparatus.	q.	Quadrate.
Fb.	Fibula.	rd.	Radius.
g.	Glenoid cavity.	re.	Radiale.
h.	Humerus.	st.	Summit of tarso-metatarsus.
i', i'', i'''.	Second metacarpal and index digit.	Tt.	Tibio-tarsus.
		ue.	Ulnare.
		ul.	Ulna.

Fig. 1. Left lateral view of skull, and detached mandible of *Conurus carolinensis*, ♂. Life size from the specimen.

Fig. 2. Mandible of *Conurus carolinensis*; seen from above. Life size, same subject.

Fig. 3. Skull of *Conurus carolinensis*. Seen upon superior aspect. Life size from the same specimen. The mandible has been removed.

Fig. 4. Under view of the skull of *Conurus carolinensis*; mandible removed. Life size, same specimen as before.

Fig. 5. The hyoidean apparatus of *Conurus carolinensis*. Seen from below, same specimen, $\times 2$.

Fig. 6. Anconeal aspect of left pectoral limb of *Conurus carolinensis*. Life size, same subject. Bones somewhat dislodged, and moved to show them to best advantage.

Fig. 7. Palmar aspect of left humerus of *Conurus carolinensis*. Life size, same specimen.

Fig. 8. Right lateral view of sternum of *Conurus carolinensis*. Life size, from the same specimen as before.

Fig. 9. Right lateral view of the pelvis of *Conurus carolinensis*. Life size, same specimen as in the former figures.

Fig. 10. Superior aspect of pelvis of *Conurus carolinensis*. Life size, same bone as shown in fig. 9.

Fig. 11. Anterior aspect of left femur of *Conurus carolinensis*. Life size.

Fig. 12. Anterior aspect of left tibio-tarsus, fibula, and patella of *Conurus carolinensis*. Life size.

Fig. 13. Anterior aspect of left tarso-metatarsus of *Conurus carolinensis*, showing also basal and summit views of the same bone. All these bones, including the foot (fig. 16), are taken from the same specimen used for the former figures. Life size.

Fig. 14. Right lateral view of the five vertebræ and pygostyle constituting the skeleton of the tail of *Conurus carolinensis*. Life size, same specimen.

Fig. 15. Superior aspect of left scapula of *Conurus carolinensis*. Life size, same specimen as in former figures.

Fig. 16. Inner aspect of left pes of *Conurus carolinensis*. Life size, same specimen.

Fig. 17. Right coracoid and os furculum of *Conurus carolinensis*, seen from behind. Life size, same specimen.

Fig. 18. Sternum of *Conurus carolinensis*. Pectoral aspect. Life size, same bone shown in fig. 8.

A NAVAJO SKULL. By R. W. SHUFELDT, M.D., *Captain Med. Corps, U.S. Army, Membr. A.O.U., Membr. Soc. Nat. E.U.S., Membr. Scientif. Socs. of Washington; Cor. Memb. Soc. Ital. Antropologia, Etnologia, e Psicologia Comp., Florence.*
(PLATE XII.)

It is a well-known fact that for many years past the majority of descriptive anthropotomists, in describing the skull, have divided the bones composing it into those of the *face* and those of the *skull*. So that if we adopt the nomenclature of Dr J. Barnard Davis, the valuable and interesting specimen which forms the subject of this paper would be considered a *calvaria*, as it lacks the lower maxilla. According to this authority, too, a *cranium* was regarded as being composed of the entire number of bones of the head and face, while the *calvaria* was made up of the bones of the skull alone. In these days, when the knowledge of the general structure and physiology of vertebrates has become absolutely indispensable to the anatomist, be his particular line of research what it may, such artificial landmarks are gradually becoming obsolete.

At the best of times Navajo Indian skulls are difficult objects to obtain, so I considered myself particularly fortunate when some time during the early autumn of 1885 the present specimen came into my possession. It was collected by a young man on one of their burial grounds upon the hills in the vicinity of Fort Wingate, New Mexico, and handed to me immediately afterwards to make such use of it as I saw fit.

This skull is from a male subject of about forty years of age, who came to his death by a gun-shot wound of the head. The results of this fatal injury are not far to seek in the specimen, and they may be seen in part in my illustrations of it in the Plate.

We find the large wound of entrance has pierced the left outer angle of the supraoccipital bone, and destroyed the adjacent mastoidal process of the *pars mastoidea* of the temporal, resulting in a magnificent example of that rare condition, a

fracture by *contre coup*, the external appearance of which may be seen upon the right frontal bone in three of the figures.

Five years ago, when Otis published the list of the human crania contained in the Anatomical Section of the United States Army Medical Museum, this extensive and unrivalled collection of several thousand specimens had in it but twenty-two, perfect or imperfect, Navajo Indian skulls.

At present this collection is not available to me, but from the excellent catalogue in question, I am enabled to select certain data of the highest value for comparison with similar observations made by myself upon the specimen in hand.

Of the twenty-two skulls alluded to I have chosen eight as nearly perfect ones as possible, and of the same sex as our subject, with a slight variation in age. From the data afforded by these in the catalogue, the averages exhibited in the sub-joined table, for comparison with corresponding ones in our specimen, have been computed. Very wisely, Dr Otis adopted the metric system in all of his measurements, and the same is employed here. At the headings of the several columns of the table I have used certain abbreviations; among these, where an explanation seems necessary, "*Cran : cap. c.c.*," stands for cranial capacity in cubic centimetres; *C* is the circumference taken (in my case) with a steel metric tape measure, upon the periphery of the figure formed by the plane which passes through the glabella, the occiput, and outstanding lateral points; *F* is facial angle; *L* is longitudinal diameter, from glabella to highest point of occipital prominence; *H* refers to the height, measured from the middle of the anterior margin of the foramen magnum to the highest point on the cranial vault; *ZD*, is the zygomatic diameter; and finally, *B*, the greatest transverse parietal diameter, or the breadth.

During the time Dr Otis lived (and it was my good fortune to see many of the human crania there measured while he had charge of that part of the Museum) No. 8 shot was the medium by which the internal capacity of the specimens was ascertained; but since then methods involving greater accuracy have been adopted.

As I have already stated, circumferential measurements were obtained from the specimen in my hands by a flexible steel

tape measure, while diameters were taken with an accurate pair of calipers. In computing the cranial capacity, I filled all the foramina leading into the brain case so carefully that the fillings were made flush in every instance with the internal cranial wall. After this was done the skull would contain water without leaking, but instead of using that vehicle, I employed the shot known to collectors as "dust

Table of Averages.

Museum No. of Specimen.	Age and Sex.	Cran. Cap. c.c.	C. mm.	F.	L. mm.	H. mm.	Z. D. mm.	B. mm.
788	35, ♂.	1480	519	77°	180	137	142	148
97	30, ♂.	1190	479	79°	164	124	127	140
130	45, ♂.	1335	495	77°	168	133	129	144
134	35, ♂.	1480	511	...	183	142	...	137
633	30, ♂.	1325	499	76°	175	138	125	130
784	40, ♂.	1550	513	74°	182	144	139	136
785	55, ♂.	1435	490	77°	163	140	138	148
1086	45, ♂.	1560	521	82°	187	138	143	142
Averages.	39+	1419+	503+	77°+	175+	137	134+	140+
Data from the present Specimen.	40+	1520	527	80°	169	151	150	160

shot" (smaller than No. 12). It will at once be seen that this gives a higher figure, yet at the same time a more accurate result than No. 8 shot can do, as used by Dr Otis. Quicksilver would come still nearer the mark, as it would perfectly accommodate itself to all the surfaces of the walls bounding the cranial casket within. In consulting the above "Table of Averages," the fact that I used smaller-sized shot in taking the cranial capacity must be borne in mind.

Next, with an excellent camera, which I possess and employ to do work very similar to the present, I photographed this calvaria in four different positions, and from these photographs, by a process in which inaccuracy is reduced to a minimum, I made the four drawings presented in the Plate.

So far as any single specimen of a skull can be, this one, no doubt, is typical of the skull as found in the Navajo Indians—at least for the adult male portion of them.

In past times the field of study in human craniology was

rather an unsatisfactory and discouraging one, owing to the fact that the greatest diversity was found to exist among skulls representing individuals of the same race; but now, thanks to composite photography, the vista which opens before us is far more hopeful. Especially is this true of Galton's methods of comparing the *components* with the *composite*. After the ideal composite has been formed by the proper employment of the eight types of components, we then have the starting point from which generalised data may be deduced, and subjects such as the present can be advantageously compared. By comparing the figures with the data in the table, and the latter for the several specimens introduced, much may be brought out of a very suggestive nature, even in such a brief sketch as I here offer—indeed, a great deal which falls without its proper scope, as originally intended, which was simply to illustrate by measurements and drawings the leading characteristics of an adult male skull of a representative of one of the most prominent tribes of existing North American Indians.

DESCRIPTION OF PLATE XII.

Fig. 1. Calvaria of Navajo Indian, ad. ♂, nearly direct anterior aspect, considerably reduced from the original.

Fig. 2. The same specimen seen from above.

Fig. 3. A rear view of the same upon a somewhat larger scale than employed in figs. 1 and 2.

Fig. 4. The same specimen, lateral view, the scale being the same as in fig. 3.

ADDITIONAL NOTE ON THE NAVAJO INDIAN SKULL.

By Professor Sir WILLIAM TURNER, M.B., F.R.S.

As Dr Shufeldt has very kindly sent me the Navajo skull, described in his paper, for presentation to the Anatomical Museum of the University of Edinburgh, I have had the opportunity of examining this interesting specimen, and wish to supplement his description with a few additional particulars.

The skull presented a well-marked parieto-occipital flattening, obviously due to artificial pressure, which had been applied so as to cause the suprasquamous part of the occipital bone and the posterior $\frac{2}{3}$ ths of the parietal to slope upwards and forwards. The frontal region did not exhibit any flattening, so that in this individual, and it may be in his tribe of Indians, the pressure applied in infancy was apparently limited to the back of the head. Owing to this artificial distortion, the longitudinal diameter of the head was diminished, and the cephalic index, 94.6, computed from Dr Shufeldt's measurements of the length and breadth, was therefore higher than it would have been in an undeformed skull. The cranium was hyperbrachycephalic.

The height of the skull was also very considerable, and reached, as may be seen from the table, 151 mm.; the vertical index was 89, so that the skull was hyperakrocephalic. In all probability the pressure during infancy, which shortened the skull in its antero-posterior direction, forced the vertex upwards and added to the height of the cranium, so that the high vertical index was occasioned both by diminished length and increased height.

The skull was cryptozygous, for not only was the breadth in the parietal region great, but the stephanic diameter was 137 mm. The glabella was not very prominent, but the supraciliary ridges were thick and strong. The bridge of the nose was concave forward, so that the tip projected to the front. The basi-nasal diameter was 105 mm.; the basi-alveolar 98 mm.; the gnathic index was 93, and the skull was orthognathic. The nasal spine of the superior maxillæ was moderate. Where the side walls of the anterior nares joined the floor, the margin of the opening

was rounded. The transverse diameter of the orbit was 40 mm.; the vertical diameter 36 mm.; the orbital index was 90, and the orbit was megaseme. The nasal height was 48 mm.; the nasal width 25 mm.; the nasal index was 52, and the nose was mesorhine. The palato-maxillary length was 56, the palato-maxillary width was 72 mm.; the palato-maxillary index was 128, and the roof of the mouth was brachyuranic.¹ The teeth were all erupted and not much worn. The cranial sutures were all unossified. The parieto-sphenoid suture in the pterion was 19 mm. in antero-posterior diameter. There were no Wormian bones. The anterior end of the inferior turbinated bone was almost in the same plane as the anterior nares.

¹ See my Report on Human Crania in Reports of "Challenger" Expedition, part xxix., 1884, for the introduction of this term.

ON THE ORIGIN OF CERTAIN CYSTS—OVARIAN,
VAGINAL, SACRAL, LINGUAL, AND TRACHEAL.
By J. BLAND SUTTON, F.R.C.S., *Erasmus Wilson Lecturer
on Pathology, Royal College of Surgeons, England.* (PLATE
XIII.)

IN the present communication the mode of origin of certain forms of ovarian cysts will be considered, also the relation of Gartner's ducts to vaginal cysts, and the part played by the post-anal gut in producing congenital sacral cystic tumours. Some remarks will also be made on lingual and tracheal cysts.

The material which has supplied me with the facts to be recorded in this communication concerning the ovaries and Gartner's ducts consisted of the uterus and its appendages taken from seventy cows, varying in age from nine months to ten years. Many of these were virgins or heifers, others had borne several calves, and many of the specimens were pregnant at the time of dissection. These uteri were obtained from animals slaughtered for the purposes of food; all the specimens were taken consecutively, so as to represent as far as possible average conditions.

At the same time, and under precisely similar conditions, the uterus and appendages were examined from fifty sows. Also the generative organs of twenty aged mares, in addition to fifty reported upon last year.

These specimens are supplementary to the great number of animals which come under my observation at the gardens of the Zoological Society.

The dissection of these specimens was undertaken for the purpose to trace, if possible, the mode of origin of ovarian cysts, and the relation of Gartner's ducts to cysts of the broad ligament, and the upper part of the vagina.

Ovarian Cysts.

I do not propose to spend time in discussing the various theories that have been raised to explain the mode of origin of ovarian cysts. Nearly everything that enters into the com-

position of this wonderful organ has been pressed into the service. Briefly, my aim is to show in no uncertain way the mode of origin of some of the cysts.

In this *Journal* (vol. xix. p. 139) I drew attention to the fact that two-thirds of all mares that attain the age of eight years present cystic ovaries, the cysts varying in size from a grape to an orange: it was also stated that some of these cysts probably arise in Graafian follicles, and that others are of parovarian origin. After the publication of the paper referred to, I still pursued the investigation, and was fortunate enough to encounter in the ovary of a mare, a cyst of the size of a nut occupying the centre of a large corpus luteum. This specimen is figured and described in the *Trans. Path. Soc.*, vol. xxxvi. This case seemed to support the view that there is reason to believe in the origin of some ovarian cysts in degenerate corpora lutea, that I resolved to pursue the question in the ovaries of cows, for, of all domestic animals, they seem to be the most liable to ovarian cysts. Accordingly, seventy sets of generative organs were obtained from these animals.

The result of the investigation was eminently satisfactory, for it goes to show in a most conclusive manner that ovarian cysts do arise in corpora lutea.

In fig. 1 (p. 434) the various stages are represented as follows:—

- A.—A section through a normal ovary from a heifer; the small cysts are immature Graafian follicles.
- B.—A corpus luteum of pregnancy. The uterus contained a calf about two months old in the corresponding uterine cornu.
- C.—The centre of the corpus luteum in this case is occupied by two distinct cavities, lined by a delicate membrane, and containing fluid. Two distinct cavities are only occasionally present in one corpus luteum.
- D.—In this stage the cavity has attained the size of a nut; two old cysts of similar organ are also seen in the ovary.
- E.—The cyst here represented was of the size of an orange, and filled with fluid. Its relation to the preceding cysts is demonstrated indubitably by the circumstance that the same yellow-coloured material forms a lining to the cyst immediately beneath the peritoneal investment.

In addition to the principal cyst, a number of smaller ones may be seen on its sides. It is important to draw attention to this, for they may be mistaken to represent secondary cysts, whereas in reality they are cysts similarly developed in old

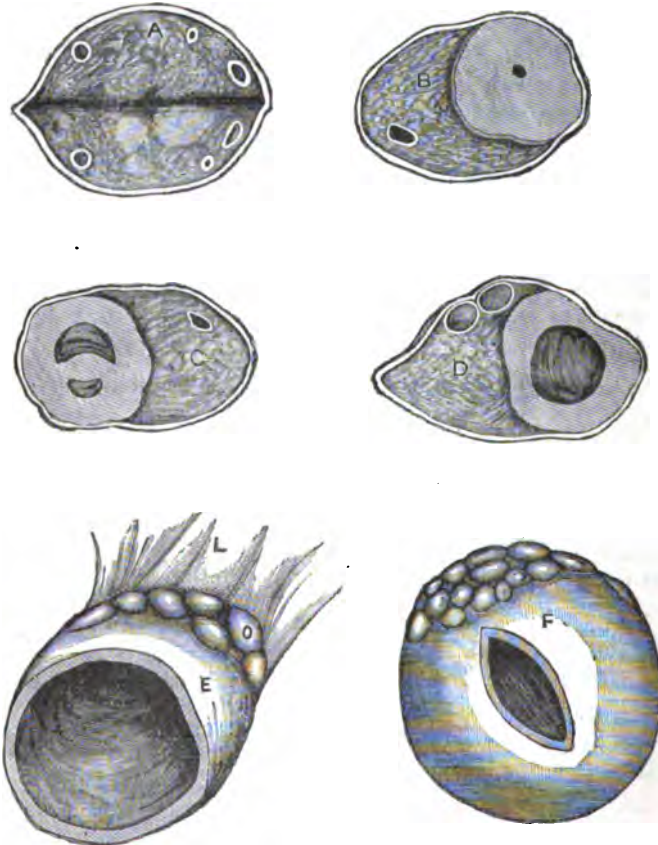


FIG. 1.—A series of drawings to show the origin of ovarian cysts in corpora lutea. Figs. A to E are from the ovaries of cows. F represents a cyst which occurred in the ovary of a tiger.

corpora lutea, but quite independent of the larger one; they form part of the cyst wall because they, with the ovary, became flattened out and incorporated with the cyst walls, due to the pressure of the abnormal mass. I have been able thus to account for similar multiple cysts in the human female.

This series supplies evidence beyond all dispute of the gradual formation of a cyst from a corpus luteum. Evidence is not wanting to show that if two or more corpora lutea in the same ovary become cystic, and this is far from being uncommon, a multilocular cystoma may arise. To me, the most satisfactory feature of the investigation is this,—anyone with a little patience may obtain twenty-five cows' ovaries and demonstrate all the stages represented in fig. 1 with the greatest of ease, and without any other assistance than that afforded by a sharp knife.

Besides in cows, the process may be traced in mares and in pigs, but not so readily as in cows. Cysts also occur after the same fashion in tigers, and one of fair proportions from this animal is shown in woodcut 1, F. Other observers have suggested that the same process holds good for human females, and I have seen specimens which support these observations in women and in monkeys.

One other question suggests itself. In the specimens figured the cysts occurred for the most part in animals which had borne young. Do the same statements hold good for virgins? It may be mentioned that old animals or those which had borne young were selected, because the corpora lutea were larger, and illustrated the condition more clearly, but virgins are also liable to precisely the same changes in all the species dissected.

It is now essential that we should endeavour to explain why these bodies should soften in the centre and form cysts. Fortunately a very satisfactory explanation is forthcoming. In the ripe ovarian follicle we can distinguish a distinct wall derived from, and continuous with, the stroma of the ovary. The inner aspect of the boundary wall is lined by layers of epithelial cells forming the membrana granulosa. Similar cells surround the ovum, but are polyhedral or columnar in shape; a collection of cells usually forms at one part known as the discus proligerus. When the ovum escapes from the follicle the cavity becomes filled with effused blood. After a time (about fourteen days) the blood clot is in a great measure replaced by a material of a distinct yellow colour, forming the well-known corpus luteum. This tissue is present in corpora lutea of menstruation and of pregnancy, the only difference being one of quantity.

It is by no means a decided question as to the source of the yellow material. Under the microscope it presents cells of various shapes and sizes intersected by capillary blood-vessels derived from the wall of the follicle, the tissue according to one observer resembling the cortical substance of the supra-renal capsules. There are three possible sources of this tissue :—

(1) It may arise from proliferation of the cells of the membrana granulosa, or (2) be derived from the follicular wall ; (3) it may result from the organisation of the blood-clot.

For my own part I think it is due to the two last causes combined. Certainly the clot is in an exceedingly favourable condition for organisation. Whichever view is the true one the following fact remains inviolate, viz., the centre of a corpus luteum is usually occupied by the *débris* of the original clot, which is in a gelatinous condition, the material becomes surrounded by a delicate membrane formed by the coalescence of some of the cells composing the yellow tissue. *It is by subsequent distension of the space thus formed that cysts arise so frequently in these bodies.*

With regard to the ovaries of the sows it is unnecessary to enter into details. The origin of cysts from degenerate corpora lutea could be traced as easily in them as in the cows, with the exception that the cysts do not attain so large a size relatively. Fig. 2 represents the ovary of a sow, showing numerous cysts

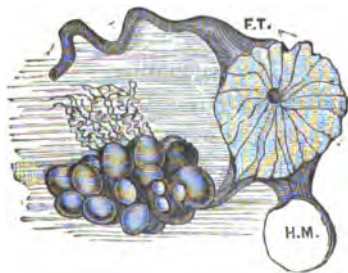


FIG. 2.—Ovary and Fallopian tube of a sow.

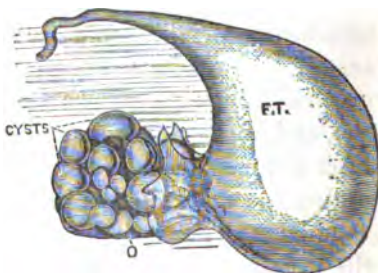


FIG. 3.—An ovary and Fallopian tube of a sow, showing hydrosalpinx.

which have arisen in corpora lutea, for in the case of these animals six or seven ova escape from each ovary at the time of *heat*, producing as many corpora lutea. In fig. 3 is represented also a sow's ovary studded with cysts, and at one end of

the organ the Fallopian tube has become firmly attached by strong adhesions, and in such a way that its ostium abdominale is completely occluded. As a result of this, the tube has become dilated so that the little finger could easily be accommodated in its interior. The natural dimensions of the tube are represented in fig. 2.

On carefully examining the Fallopian tubes of all the sows (fifty in number) three well-marked cases of distention of the tube were found, constituting veritable cases of hydrosalpinx. In all cases the abdominal end was firmly adherent to the ovary, and completely occluded. In my previous paper a case of pyosalpinx was described which occurred in a kangaroo; a second specimen has since come to hand. Now that the affection has been found also in pigs and in the cow, there can be little doubt that, if carefully looked for in other mammals, by those who have opportunities, other cases will doubtless come to light.

Before leaving the ovary it will be of interest to consider further certain details connected with the "tissue of the hilum." For several months I have systematically examined the ovaries of every female human foetus, from the eighth to ninth month of intra-uterine life, which has come into my room for dissection. The ovaries were preserved entire in Müller's fluid in the usual way, and when properly hardened were cut into sections for the microscope. In this work I was fortunate enough to have the assistance of three of my pupils—Messrs Sibley, Nash, and Marris—in cutting and mounting many of the specimens.

The results of this work will be briefly stated. In all cases the "tissue of the hilum" was very conspicuous, but varied considerably in amount. It consists chiefly of connective tissue, containing a very large number of veins. These veins, later in life, may undergo abnormal dilatation, constituting varicocele in the female, which is in every respect analogous to the same condition occurring in relation with the testicle.

In the majority of the ovaries examined, the tubules constituting the parovarium could be traced with ease into the substance of the ovary, but they were in the majority of cases entirely confined to the hilum of the organ. Associated with the tissue of the hilum are relics of the mesonephros (Wolffian

body), named by Waldeyer "the paroophoron." The paroophoron agrees histologically as well as in the matter of development with the paradidymis (organ of Giraldés.) Critical examination of the "tissue of the hilum" has served to convince me, not merely that it contains remains of the mesonephros, but that the connective tissue composing it is derived directly from the degeneration of that organ.

It occasionally happens that at birth an ovary will be found divided by a deep longitudinal furrow. In some of these specimens the furrow actually divides the ovary into two histologically distinct parts—parenchyma, and mesonephritic remains. This is very well seen on Plate XIII. fig. 1, where the part P represents true ovarian stroma, and O a very large paroophoron: the section being carried across the two edges of the longitudinal furrow before referred to.

In one case in which the ovary was found to be cystic, some of the cysts being as large as a pea, the remains of the mesonephros exceeded the bulk of the true ovarian stroma three times.

The transverse section (that is, in the direction of the minor axis) of the foetal ovary on Plate XIII. fig. 2, represents another example of an excessive amount of mesonephritic tissue. In this instance the foetus was anencephalic. In this ovary, as well as in the one represented in fig. 1, the distinction between the two parts was so obvious that it was easy to determine the parenchyma from the "tissue of the hilum," when the sections were made transparent and fixed upon a slide.

The relation of the various parts of the ovary to each other, and to cystic formations occurring in that organ, are represented in Plate XIII. fig. 3. This figure has been compounded from a series of sections of a human ovary at the ninth month. It is intended to show the parenchyma, with a ripe ovum lying in a follicle, also a corpus luteum. Running into the hilum are several parovarian tubules, and lying among them is an incipient papillary cyst, which is prone to occur in this part of the ovary.

Seeing that the "tissue of the hilum" really has its origin in, and often contains the remains of part of the mesonephros, and is really equivalent to the structure named by Waldeyer "paroophoron," it seems unnecessary to employ the term "tissue

of the hilum," but to regard the ovary as being compounded of two parts, *oophoron* and *parooporon*.

The investigation has not only been interesting concerning the relation of the tissue of the hilum to the paroophoron, but it surprised me in the very large proportion of foetal ovaries which present a cystic condition at birth. I have already seen seven examples, out of a total of more than forty foetuses, which have been specially examined in regard to this point. After birth, doubtless, many of these cysts disappear, or cause no trouble; nevertheless, there can be little doubt that many ovarian cystomata which later in life give trouble, had already commenced their growth in the ovary at the time the unfortunate individuals who possess them commenced their extra-uterine existence.

BROAD LIGAMENT CYSTS.—In a criticism on my previous communication regarding cysts in connection with the reproductive organs of animals, in this *Journal*, vol. xix. p. 121, Mr Doran suggested that in all probability some of the cysts described as parovarian in origin might really be simple broad ligament cysts, unconnected with the parovarian tubules. An examination of some fresh ovaries of mares has convinced me that some of the cysts found in the mesosalpinx are unconnected with the parovarium. On Plate XIII. fig. 4, is shown the Fallopian tube of a mare with three of these cysts *in situ*: they were situated between the layers of the mesosalpinx, possessed thin walls, and were filled with fluid. Running among the cysts and in relation with one of them are large dilated lymphatic vessels. These lymphatic vessels in cases of obstruction caused by cysts are easy of detection, for immediately after death the lymph coagulates, and they become distended as by a natural injection. Probably many, but not all, simple broad ligament cysts arise from dilatation of lymphatic channels.

Gartner's or Gaertner's Ducts.

Whilst engaged in examining the generative organs of cows, I seized the opportunity of further testing the question as to the probability of cysts of the broad ligaments and of the upper part of the vagina arising in these ducts or their rudiments.

The material was exceedingly favourable for the investigation,

because in cows these ducts attain, so far as female mammals are concerned, a very high development. Among the seventy specimens the following variations in the condition of Gärtner's duct were met with.

In all young animals both ducts were present as pale streaks on the ventral wall of the uterus, immediately beneath the peritoneum. In the majority of the specimens they became gradually incorporated with the tissue of the cervix uteri, their lumen gradually suffering obliteration at this point; in some cases, but quite exceptionally, they opened on the mucous surface of the vagina, midway between the os uteri externum and the meatus urinarius. Anteriorly these tubes were continuous with the longitudinal tube of the parovarium. In older cows the ducts in some cases disappear in various parts of their course, in a few instances completely. The persistent portions of the tube, however, dilate, especially in the neighbourhood of the cervix and vagina, forming tubulo-cysts, which in some cases are as large as an orange, and bulge into the vagina. In cows which have borne several calves, the ducts in relation with the cervix exhibit extreme thickening of the walls, as though from chronic inflammation. If the ducts remain pervious throughout their whole length they increase in dimensions with the uterus, often attain the size of a quill pen, and are filled with fluid resembling serum.

There is yet one other point of some interest to be considered in relation to the mode of termination of these ducts in the vagina. Anatomists had long been of opinion that two minute openings in the human vagina, near the opening of the urethra, represented the terminal orifices of Gärtner's ducts, which have become familiar as Skene's tubes. Further attention was centred upon them when it was found that they are liable to inflame and lead to trouble in the human subject. Recently, however, the relation of the orifices to Gärtner's ducts has been questioned by Dr Schüller¹ and others, and the openings have been described as belonging to two glands lying in the wall of the vagina, near the termination of Gärtner's ducts. A knowledge of these opinions induced me to write cautiously on the mode of termination of the ducts in my previous papers on the subject, until

¹ See Doran, *Tumours of the Ovary*, page 43.

leisure and opportunity should enable me to inquire into the matter afresh.

It is a fact thoroughly established that the vasa deferentia of the testicles are the male representatives of the ducts of Gärtner in the female. Immediately before the vasa terminate on the floor of the urethra two diverticula are found, the vesiculæ seminales. In virgin cows a similar but very much smaller diverticulum arises from the end of Gärtner's duct, and is situated in the wall of the vagina. In very many cases the duct, immediately above the glandular diverticulum, often becomes obsolete as mentioned before. Under such conditions a thin probe passed into the orifice of the duct when existing would lead into the gland, but not into the duct above, and thus give rise to the fallacy of the independence of the gland in question from Gärtner's duct. See woodcut 4.

In this diagram (1) represents the vas deferens in its relation to the vesicula seminalis. (2)

Shows the duct of Gärtner and the glandular diverticulum I have described, the diverticulum bearing the same relation to the duct as the vesicula seminalis does to the vas in the male. (3) This is intended to represent a not uncommon condition of the glands

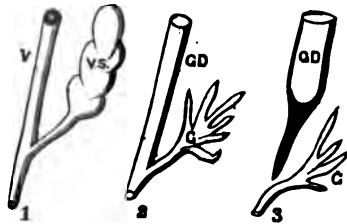


FIG. 4.

1. The Vas deferens and vesicula seminalis. 2. Gärtner's duct and its diverticulum. 3. The terminal orifice and diverticulum of Gärtner's duct in its most common condition.

in question; the tube becoming impervious immediately above the spot where the gland-duct joins the tube. This arrangement clearly explains the apparent independence of the gland and Gärtner's duct. Judging from the number of specimens I have dissected, it is easy to understand, from the frequent amount of mucoid fluid they contain, that they could easily become involved in local catarrhal inflammation, and lead to considerable annoyance. But that they are independent of the ducts of Gärtner is erroneous.

From the foregoing statements the following are the chief inferences which may be drawn:—

1. In cows, mares, pigs, tigers, goats, and human beings, some

cysts of the ovaries arise in corpora lutea either of pregnancy or of menstruation. Waldeyer, Beigel, and De Sinéty have pointed out that even before birth the ova ripen, atrophy, and form a kind of corpus luteum. I have had ample opportunities of confirming these statements, and have convinced myself that the process goes on throughout childhood, and gives rise to cysts.

2. Pigs and cows, as well as kangaroos, are occasionally liable to dilatation of the Fallopian tubes due to adhesion of the fimbriated end to the ovary. *Hydrosalpinx*.

3. Gärtner's ducts are potential sources of vaginal cysts.

4. Skene's tubes (so-called) are diverticula of Gärtner's ducts, and represent in the female the vesiculæ seminales of the male.

Sacral Cystic Tumours.

A vast number of tumours, varying in character from a simple cyst to a more or less fully formed individual, have been placed on record as occurring in connection with the sacral and coccygeal regions of human beings. The term sacral tumour has been used by pathologists in a generic sense to include all the varieties of these singular formations.

Within the last few years some observations have been recorded which tend to throw some definite light on these cases and recent advances in the science of embryology, especially in connection with the caudal extremity of the embryo, offer clear explanations of the cystic varieties of sacral tumours.

In the first place it must be pointed out that it is necessary to separate the various tumours into classes.

Braune, who has collected a vast number of these cases (95 in all) in his admirable monograph, *Die Doppelbildungen und angeborenen Geschwülste der Kreuzbeingegegend*, 1862, divides them thus:—(1) Parasitic, or attached fetuses; (2) Hygromata, or cysts; (3) Lipomata. The first of these three groups I do not propose to consider, but the cystic formations and lipomata will claim especial attention.

Braune clearly recognised that among the sacral hygromata we have to deal with two distinct varieties, one form arising as a dilatation of the caudal extremity of the spinal meninges, the other he endeavoured to account for rather fancifully, as arising from the degeneration of Luschka's coccygeal gland.

The first type case is from a preparation preserved in the Meckelian Museum at Halle. The tumour was attached to the lower sacral region, and measured 10 c.m. in length, 6 c.m. in breadth, and hung pendant by a pedicle 1 c.m. in thickness. The details of its relation to the vertebral column are shown in fig. 5. An accurate dissection of the relation of the coverings

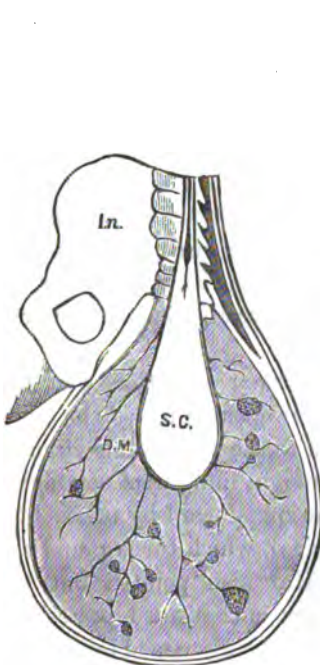


FIG. 5.—A congenital sacral cystic tumour due to dilatation of the terminal portion of the spinal meninges. (After Braune.) s.c., spinal canal; D.M., dura mater.

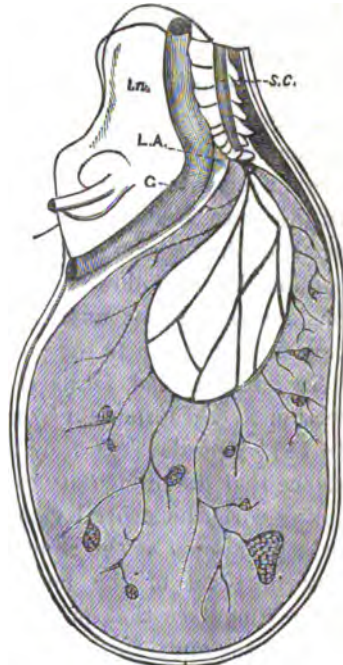


FIG. 6.—Congenital cystic sacral tumour lying anterior to the sacrum. (After Braune.) I.n., innominate bone; s.c., spinal canal; L.A., levator ani; G., gut.

of the tumour to the fascia, &c., of the trunk was not possible on account of the long soaking of the specimen in spirit. The following points, however, could be made out with certainty. The central cavity of the tumour was in relation with the spinal canal, as in the case of a spina bifida, but with this difference, the communication occurred through the normal *hiatus sacralis*. The walls of the cyst were made up of skin, fascia, connective

tissue, muscle fibre, and a fibrous lining to the cyst resembling the dura mater.

The second type case was also preserved in the Meckelian collection at Halle. It was a seven months' female foetus, which had long been preserved in alcohol. The anatomical details are shown in woodcut 6. In this instance the tumour is unconnected with the spinal canal, which is completely closed, and lies on the anterior (ventral) aspect of the coccyx. Between it and the rectum is the levator ani muscle, and a fibrous envelope which surrounds it is directly continuous with the coccygeal periosteum. The centre of the mass is traversed by trabeculae giving rise to a cystic condition. It is this form of sacral congenital tumour that is often described as sarcomatous. In this case Braune considers the tumour to have arisen as a result of the degeneration of Luschka's coccygeal gland; in this opinion he is followed by others. This view, however, is rendered somewhat untenable by the investigations of embryologists in relation to the post-anal gut.

In adult animal forms it is the normal condition that the rectum should terminate by an external opening called the anus. In 1871 Kowalevsky¹ drew attention to the remarkable circumstance that the alimentary canal is brought into direct communication with the central canal of the spinal cord by means of a passage known as the neurenteric canal, which turns round the posterior end of the notochord. He² also pointed out the interesting fact that primarily the gut is continued posteriorly beyond the anus, this prolonged portion being named by Balfour the "post-anal gut." The general relation of the anus, post-anal gut, neurenteric, and neural canals to one another are represented in fig. 7.

Subsequent researches show that this arrangement of the primary intestinal canal probably holds good for all Chordata from amphioxus up to man.

Since the announcement of its discovery by the great Russian researcher it has been found in *Acipenser*, *Axolotl*, *Bombinator*, *Plagiostomi*, *Teleostei*, the hen, rabbit, and in the human embryo. These later observations are of great interest, for on the first dis-

¹ *Archiv für Mikr. Anat.*, Bd. vii. S. 114.

² *Ibid.*, Bd. xiii. S. 194, 195.

covery of the neurenteric canal it was thought to be a peculiar Ichthyopsidian character. Careful observations on various forms of the higher vertebrata go to show that a neurenteric passage

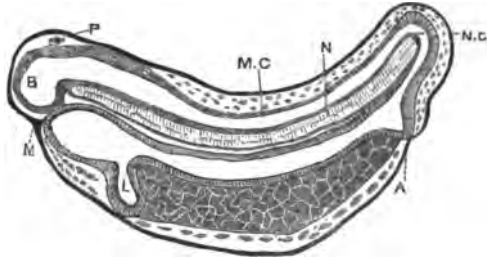


FIG. 7.—Longitudinal section of an embryo *Bombinator igneus*. A, anus; B, brain; N, notochord; M, mouth; L, liver; N.C., neurenteric canal; M.C., medullary canal (after Goette).

and a post-anal gut are characters perhaps as constant as a notochord.

For a general review of the literature of this interesting subject, and a detailed account of the embryology and structural characters of the part, the reader should consult Balfour's *Embryology*, vol. ii. pp. 267 and 634.¹ The points most important for our present purpose are the following :—

The post-anal gut is always better developed in the lower than in the higher forms of vertebrate life. In Elasmobranchs it is very well developed, and persists during a considerable portion of embryonic life, and at one period presents itself as a terminal vesicle at the end of the tail, but communicates by a narrow neck with the neurenteric canal. These curious relations of parts have led embryologists into some very interesting speculations regarding the original position of the anus, but interesting as they are, we cannot further follow them in connection with this subject. The first attempt to associate the origin of sacral cysts with post-anal gut was that by Middeldorpf,² who, in reporting a case of congenital sacral cyst, consulted Wiedersheim in relation to the development of the parts in animals. This induced him, in the paper mentioned, to connect the cyst with developmental conditions, and he further

¹ Balfour's *Development of Elasmobranch Fishes*, p. 91 and 218, may be consulted with advantage.

² *Virchow Arch.*, Bd. 101, p. 87.

points out that abnormal dilatations of this section of the gut belong to the same category as cases of abnormal persistence, and in many cases, undue dilatation of a vitelline duct.

The lining tissue of the cyst was also confirmatory of the opinion of Middledorpf as to the origin of the cyst, for it not only presented a similar structure to gut under the microscope, but *solitary follicles* were also present in great quantity.

This case is an eminently satisfactory one, but it only disposes of a part of the question; nevertheless it proves that certain cystic sacral tumours may arise in connection with the post-anal section of the alimentary canal. We must now consider some of the arguments which associate a few of these cystic tumours with the medullary canal.

Virchow's Archiv, Bd. c. s. 571, contains an article written by the great pathologist who edits the *Archiv*, entitled "Ueber einen Fall von Hygroma cysticum gluteale congenitum." In this instance Virchow received from Dr Ludwig Wolff a tumour, apparently a lipoma, which had been extirpated from the gluteal region of a new-born negro child. Its appearance and situation is represented in the accompanying drawing (fig. 8), modified from the original figure. It is in shape



FIG. 8. — Congenital sacral cystic tumour, in a new-born negro-child. (Modified from Virchow.)

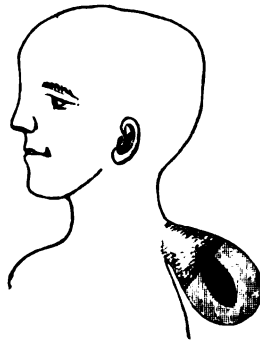


FIG. 9.

like a large fig, and measures 7·3 c.m. in length and in width 3·7 c.m. On section the interior was found to be occupied by two cysts. The walls of the tumour were thick, and composed of skin externally, fibrous tissue, transversely striated muscle fibre, nerve fasciculi, and arteries with thick walls. The inner wall of the cyst was lined with flat granular epithelium. From

a careful consideration of the case Virchow comes to the conclusion that we have to deal, notwithstanding its lateral situation, with a derivative from the spinal sheath. As in the variety of these cysts previously considered, we have positive evidence that hygromata may be derived from the hernial protrusions of spinal membranes, as in *spinæ bifidæ*; the sac may become pedunculated, the pedicle finally close, and the sac become separated from the spinal sheath, as is shown in the specimen represented in the diagram (fig. 9).

The case from which this diagram has been constructed was the remarkable one described by Mr Solly (*Med. and Chir. Soc. Trans.*, vol. xl. p. 19). The tumour was noticed at birth, but on account of its connection with the spinal canal its removal was deferred until the patient was twenty-nine years old. It was satisfactorily removed by Mr Solly. It was united by a ligamentous pedicle to the spine, but no communication existed with the spinal canal. The section of the tumour exactly resembled the pedunculated lipomata occurring in connection with the sacrum. Three figures illustrate the case in the original paper, but the details are represented diagrammatically in fig. 9.

This second variety of sacral cyst arises in connection with the structures on the dorsal aspect of the neurenteric canal. These two cases, Middeldorpf and Virchow's, confirm Braune's views, that one form of these cysts lie anterior to the coccyx, and the other posterior, exactly as represented in figs. 5 and 6, and testify to the correctness of the view that the first variety arises as a distension of the spinal meninges. Whether, in ascribing the second variety to a degeneration of Luschka's gland, Braune is in keeping with facts must now be discussed. The arguments against this view of their origin are the following:—

(1) Luschka's gland is composed chiefly of a coil of blood-vessels and connective tissue. Congenital sacral tumours contain few blood-vessels.

(2) In carefully-examined specimens of the congenital sacral tumours of the cystic variety, the cysts and duct-like passages are lined for the most part with cubical epithelium, and are held together by young connective tissue. The epithelium is usually columnar. These two circumstances alone are sufficient to exclude the coccygeal gland as the germ which gives rise to

these tumours. On the other hand, the structure of the post-anal gut eminently accords with the histological details of the cystic masses in question.

(3) When we remember the tendency functionless ducts and tubules have to become cystic, and consider the position and often pedunculated but usually impervious connection these tumours have with the rectum, and the close agreement of the epithelial lining in the two cases, it seems to me that the evidence as to the origin of these cysts in the post-anal gut is beyond doubt, and it is a more satisfactory explanation than calling in the aid of Luschka's gland.

We must now consider the third group—lipomata. Several instances have been collected by Braune and others of the occurrence of congenital lipomata in the sacral region, and, as we saw in Virchow's case, the growth was thought to be a lipoma by the operator who removed it. From a careful consideration of many recorded cases of fatty tumours occurring in unusual situations, and of several of which I have had opportunity of examining, I ventured to publish a paper in the *Trans. Med. and Chir. Soc.*, vol. lxviii., dealing with the subject, and endeavoured to show that many of these uncommon lipomata are really to be regarded as being originally composed of higher tissues, such as muscle, nerve, &c., which, in consequence of having no function, have retrograded into fat. So in these examples of sacral lipomata; doubtless they originated as diverticula from the spinal meninges or post-anal gut, as the case may be, and the tissues covering them, muscles, nerves, &c., have degenerated into fat.

Careful consideration of the anatomical and histological characters of these tumours seems clearly to indicate that one variety arises from a dilatation of the meninges of the spinal cord; the second variety is associated with the post-anal gut, and the third group or lipomata may arise in connection with either, but seems to be more frequently associated with the spinal variety.

REFERENCES.

In addition to the eighty-six cases of sacral tumours (hygromata, lipomata, spinal diverticula and coccygeal gland ? tumours) recorded by Braune in his classical work already referred to, the following cases may be mentioned :—

HUTCHINSON, *Illustrations of Clinical Surgery*, fas. xiii. This paper also contains several references.

SHATTOCK, *Trans. Path. Soc.*, vol. xxxii. p. 197.

MACNAMARA, *Trans. Path. Soc.*, vol. xxxii. p. 199.

TREVES, *Trans. Path. Soc.*, vol. xxxiii. p. 285.

WAGSTAFFE, *St Thomas' Hosp. Rep.*, vol. iv. p. 213.

VIRCHOW, *Archiv*, Bd. 100, p. 571.

MIDDLEDORFF, *Virchow's Archives*, Bd. 101, p. 37.

HOLMES, *System of Surgery*, vol. iii. p. 780. 3rd edition.

The standard works of Gurlt, Förster, Ahlfeld, and of Geoffrey St Hilaire contain numerous cases of this nature.

Dermoid Cysts of the Tongue.

In the preceding account of sacral congenital tumours it seems fairly evident that we have to deal with cystic formations arising in connection with "obsolete" canals—obsolete in the sense of being disused. There are many examples of these disused canals and passages in the body, *e.g.*, the pouch of Rathke, at the top of the pharynx; the infundibulum; the branchial arches; the central canal of the spinal cord; the neurenteric passage; the post-anal gut; the tubules of the Wolffian duct, &c.

In nearly all these passages we have a striking arrangement of parts, for these canals served during some period of embryonic life to bring the three blastodermic layers, epi-, hypo-, and mesoblast, into intimate relation.

In this section I shall confine my remarks particularly to dermoids of the tongue, for in this situation the relation of teratomata to obsolete canals is illustrated in a very striking and remarkable manner.

The best account of lingual dermoid cysts, and one easy of access, is by Mr Barker, *Trans. Clin. Soc.*, vol. xvi. p. 215. Mr Barker not only gives an interesting description of a case occurring in his practice, but has collected and analysed sixteen other recorded examples, and furnishes the following rules concerning them:—

1. They may be unilateral, lying between the genio-hyo-glossi and the mylo-hyoid muscles, on one side or the other.

2. They may be central, lying between the genio-hyo-glossi muscles.
3. They may be bilateral, lying between the mylo-hyoid and genio-hyo-glossi muscles.

Histologically they consist of tough fibrous walls, with a thin, smooth lining membrane. They contain sebaceous matter and embedded hairs, and perhaps teeth.

Mr Butlin¹ says of these cysts:—"Cases in which their actual existence has been noticed soon after birth have been very few, and the very large majority of dermoid cysts of the mouth have been observed in adults, or at upwards of thirty years of age. One case has been described in which the patient was more than sixty years old." I shall now proceed to show that dermoids in the tongue receive an explanation on anatomical grounds.

Professor Wilhelm His, in a recent work, *Anatomie menschlichen Embryonen*, Heft. iii. p. 100, 1885, gives an account of a narrow duct lined with epithelium, which runs from the foramen cæcum on the dorsum of the tongue downwards, between the genio-hyo-glossi muscles, to end blindly in the hollow of the basi-hyoid. This is termed by His the lingual canal. Associated and often in connection with the duct, is a third or middle lobe to the thyroid gland. This, too, is in connection with a duct known as the thyroid canal. In embryonic life the two ducts are continuous, and constitute a canal known as the ductus thyreo-glossus.

The existence of these ducts admits of no doubt whatever. In the tongue of the human foetus at birth a thin bristle may often be passed from the foramen cæcum to the hollow of the basi-hyoid. In the adult it is best demonstrated by carefully removing the body of the hyoid bone, as shown in Plate XIII. fig. 6, then carefully dissecting the cellular tissue lying between the genio-hyo-glossi, the duct, if present, is easily found. Up to the present I have searched for the lingual duct fourteen times, and found it present in a complete form thrice; in other specimens it could only be distinguished in parts of its course, but in the majority of cases no trace of it could be detected except the foramen cæcum, and in some specimens even this recess was wanting.

¹ *Diseases of the Tongue.*

The morphology of this duct I do not propose to consider at present, for it will be essential to work out its leading features as far as possible in a variety of mammals. The interest it has for us in this paper is that, as in the case of sacral congenital tumours and pituitary teratomata, dermoids of the tongue occur in the immediate neighbourhood of, if not in some way connected with, an obsolete canal, which traverses a large mass of mesoblastic tissue and brings the buccal epiblast and the hypoblast of the branchial clefts into intimate relation.

It is of course possible that these cysts arise in the same way as cutaneous proliferous cysts, occurring at the angle of the orbit, between the dura mater and the skull, and on the bodies of animals (see Plate XIII. fig. 5), viz., that they are involuted islands of superficial epiblast, which play the part of tumour germs. In the case of the skull we know that the skin and dura mater are in embryonic life in contact, an association which becomes disturbed when osseous material is deposited to form the skull. It is easy to see, as in a case reported by Professor Turner,¹ and more especially one by Dr Ogle,² that the cyst may have had its origin in small islands of skin left on the dura mater abnormally. In Professor Turner's specimen, although there was no visible defect in the occipital bone, as in Dr Ogle's specimen, nevertheless the cyst occurred at a spot where for a long period of intra-uterine life a defect or cleft exists in the squamo-occipital bone, and where skin and dura mater were in close relation.

Tracheal Cysts.

An interesting cyst came under my observation in an Emu, *Dromæus novæ-hollandiæ*. Before entering into the details of the case it will be necessary to give a brief account of the normal anatomy of the trachea of this singular bird.

If the integument be carefully dissected from the neck of an emu, a curious deficiency in the anterior wall of the trachea will be exposed, usually corresponding to a variable space between the fiftieth and sixtieth rings. The general aspect of this singular opening may be fairly inferred from Plate XIII. fig. 7. Although the number of tracheal rings which are defective vary,

¹ *Barth. Hosp. Rept.*, vol. ii.

² *Path. Soc. Trans.*, vol. vi. p. 12.

yet for the most part the gap rarely exceeds seven rings in longitudinal extent. The opening is about two and a half inches in length.

In connection with this aperture is a sac, varying in dimensions with different birds, according to age and sex. In an emu five weeks old I failed to find any evidence of a sac, the defect in the trachea being a mere slit; in the young emu the sac is of insignificant size, but exact observations are yet required to decide whether it differs in capacity in the male and female; but there is some probability that this is so. In adult birds of this species the sac attains considerable dimensions; in one case, according to Knox, the cyst was as large as a man's head. In Dr Murie's case the sac measured fourteen inches in its greatest length. The walls of the sac are composed of white fibrous tissue, its exterior being overlaid in parts with striped muscle fibre in very thin layers; the inner layer is continuous with the mucous membrane of the trachea, and they become continuous with each other through the tracheal opening, indeed the sac could well be described as a "hernia of the tracheal mucous membrane through a deficiency in the anterior walls of the wind-pipe," for such it seems to be. As far as could be made out in my specimen, the epithelium was flattened on the surface, but spheroidal in the deeper layers. There were small glands (mucous) dotted over the membrane. During the pairing season the bird distends this sac with air, and it is due to the chamber thus formed that these birds are able to make the curious drumming noise so characteristic of them. For all that concerns the normal anatomy of this remarkable structure the reader must refer to Dr Murie's admirable account in *Proc. Zool. Soc.*, 1867, p. 405.

Mr Bartlett invited me to examine an emu which had a large swelling in the neck, and as the bird refused food and seemed to be dying, it was deemed expedient to attempt its removal. After a severe tussle the bird was thrown; manipulation quickly informed one that it was a cyst with fluid contents, and an incision was promptly made, and the contents, which consisted entirely of mucus, evacuated. On attempting to arouse the bird, to our astonishment it was dead. Dissection made clear the cause of the fatality. The tracheal cyst, which has been described above, had inflamed and led to such an abundant

secretion of mucus that the sac had become so distended as to measure in length 18 inches and in width 14 inches. When the bird was thrown for the purpose of laying open the cavity the dependent position had caused the mucus to flow into the trachea and obstruct the bird's respiration; in fact it was drowned in its own mucus.

The cyst in the emu's neck is to be regarded as a hernia of the tracheal mucous membrane through a deficiency in the rings of that tube on its anterior aspect; in this sense it is very remarkable. Tracheal cysts in the human subject occasionally occur, but are usually found protruding through the muscular and fibrous tissue which fill up the deficient space on the posterior aspect of the trachea, and often form cavities of considerable size; in rare instances they become so large as to require surgical interference. Virchow quotes Textor as having operated in one of these cases with success.¹

That the mucous membrane of the trachea should become herniated in this way is not at all remarkable; every other similarly constructed tube is liable to the same abnormality. In the intestines false diverticula may be found. As many as two hundred have been seen in the same subject.

In the bladder the corresponding condition is known as sacculation. The œsophagus is the seat of similar lesions often. In this *Journal*, vol. ix, p. 134, Dr Morrison Watson described a large diverticulum which was connected with the pharynx, due in all probability to the same cause. Indeed, any tubular structure may become so affected, be it intestine, artery, vein, ventricle of the brain, or even the spinal cord.

The cyst of the emu has other points of interest, for it is doubtless an example of a pathological condition which has been perpetuated, so as at length to become a specific character. That this cyst is the direct result of the imperfection of some portion of the tracheal rings cannot be doubted. In the young bird the cyst does not exist, but as life advances the hernial protrusion occurs. The defect in the trachea is inherited; the escape of the mucous membrane through the opening is the necessary result.

Among all species of birds no example is known of a similar

¹ *Tumours*, French edit., vol. i. p. 263.

arrangement of the trachea such as pertains in the Emu, but the Bustard (*Otis tarda*) affords valuable testimony in support of the view here advocated regarding its origin.

At certain times of the year the Australian Bustard (*Eupodotis australis*), and the Bustard (*Otis tarda*) exhibit the peculiar phenomenon termed "showing off." In both birds during the "show off" there is a distension of the neck with air. In the case of the Australian Bustard this tube is simply the dilated œsophagus, but in the case of *Otis tarda*, according to some observers, it is due to a special sac opening under the tongue.

According to the evidence it appears that this gular pouch of the bustard is present in the adult male only, but is not a constant character. Garrod points out, however, that in the young bird there is a singular arrangement of the frænum linguæ. In the young bustard this structure, instead of being median and single, consists of two slight lateral vertical folds, with a median interval a quarter of an inch across. This arrangement is exceedingly well adapted for permitting the development of a pouch during the sexual season; when the air passages are inflated during the showing-off, the fold of mucous membrane is very weak, and the continued pressure causes it to stretch. The statement concerning the pressure is not a gratuitous assumption, as the following case will show. When dissecting a young specimen of *Otis tarda* Garrod was surprised to find what appeared to him to be a crop projecting from the posterior aspect of the œsophagus. Further investigation revealed to him the fact that this was really an abnormal diverticulum of the œsophagus, probably produced by the same mechanism that was responsible for the gular pouch.

In 1882 Mr W. A. Forbes rendered Garrod's opinion more probable by finding in an Australian Duck (*Biziura lobata*) a similar arrangement of the frænum linguæ and a gular pouch in two specimens of the male, such as is found in the adult male of *Otis tarda*.

Taking into consideration the anatomical arrangement of the frænum, the non-existence of the gular pouch in the young bird, its absence in the female, and its inconstancy in the male bird, as well as the evidence afforded by the two Australian birds (*Eupodotis* and *Biziura*), it will not be inconsistent to regard the

gular pouch as a pathological phenomenon brought about by the habit of "showing off," the tendency to cystic dilatation, or rather hernia, of this part of the buccal mucous membrane being inherited.

Further details concerning the gular pouch of the bustard will be found on reference to the following papers:—

MURIE, *Proceedings of the Zoological Society*, 1868.

GARROD, *Proc. Zool. Soc.*, 1874, p. 471, and *Collected Papers*, p. 242.

FORBES, *Proc. Zool. Soc.*, 1882, p. 455, and *Collected Papers*, p. 354.

Dr Murie's paper contains several other references of value.

EXPLANATION OF PLATE XIII.

Fig 1. Longitudinal section of the ovary of an anencephalic human fœtus at the eighth month. *P.*, paroophoron; *O.*, oophoron. The two parts were separated by a distinct furrow. [$\times 10$.]

Fig. 2. Transverse section of the ovary of a human fœtus at birth. *P.*, paroophoron, or remains of the mesonephros, unusually large; *O.*, oophoron, or true ovarian parenchyma. [$\times 10$.]

Fig. 3. Diagrammatic section of an ovary. *P.*, parovarian tubules, the seat of simple (parovarian) cysts; *Pa.*, paroophoron, the seat of papillary cysts, *P.C.*; *O.*, oophoron, the seat of cysts arising in corpora lutea, *C.L.* A ripe follicle is shown at *R.F.*

Fig. 4. Simple cysts of the broad ligament in a mare. *V.*, a dilated lymphatic.

Fig. 5. Piliferous cyst from the back of a cow.

Fig. 6. The root of the tongue and hyoid bone, to show the lingual duct. *G.*, genio-hyo-glossus; *H.G.M.*, hyo-glossus muscle; *H.*, hyoid bone; *T.H.M.*, the thyro-hyoid membrane; *T.C.*, the thyroid cartilage. Duct, the lingual duct.

Fig. 7. Tracheal cyst of the Emu. The figure shows the tracheal window.

THE BLOOD-FORMING ORGANS AND BLOOD-FORMATION: AN EXPERIMENTAL RESEARCH.

By JOHN LOCKHART GIBSON, M.D., *Formerly Senior Demonstrator of Physiology, University of Edinburgh.*
(PLATE XIV.)

(Continued from p. 353, vol. xx.)

Function of Lymphatic Glands.—The function of the lymphatic glands as regards the formation of red blood-corpuscles has in this paper already been alluded to; but it will now be necessary to consider an experiment which has a more direct bearing on this function.

After thinking over what I wished to do on the blood and drawing up a plan of work, I consulted Professor Rutherford as to whether this plan would be likely to yield results. He was good enough to draw my attention more particularly to the possible action the lymphatic glands might take in the formation of red blood-corpuscles, an action I had been inclined to doubt. He suggested that in this relation a lymphatic gland should be excised from one animal and planted under the skin of another animal, so that it might be nourished by the lymph of its host, while its own lymph would probably be confined in its interior; and that by this means one might be able to discover whether the lymph corpuscles when confined in a lymph gland for a longer time than usual would show stages of transition towards red corpuscles.

On considering this suggestion, I thought its advantages might be obtained by another method of procedure, which, although much more difficult, would probably be more certain, and would allow of other observations being made at the same time.

This other method was to tie the thoracic duct at its opening into the veins at the root of the neck, and first watch the effect on the blood before the death of the animal, and then observe the condition of the lymphatic glands after the death. I say, "after the death," because I expected the animal to die within a short time of the operation, from interference with the absorption of fat.

Experiment VIII.

A male dog of the English terrier type, weighing 5 kilogrammes 70 decagrammes. Apart from being rather thin, the animal was perfectly healthy. Must have been at least three years old.

On the 2nd of February 1885, four hours before the time proposed for the operation, the dog was given as much milk as it would drink, in order that the thoracic duct might be full of chyle at the time of operation, and so, by its white colour, help one to find it. The animal having been put under ether, a V-shaped incision was made at the lower part of the neck, one of the limbs of the incision being parallel to and just above the clavicle, and the other parallel to the posterior border of the sterno-mastoid muscle. Then I reflected back the triangular flap of skin so marked out, divided the platysma, and dissected downwards with the finger, following the course of the external jugular vein, as far as its junction with the internal jugular. To give a little more room, some of the clavicular fibres of the sterno-mastoid muscle were divided. In this way one got deep down behind the clavicle; and after separating the structures as gently as possible, one noticed what appeared to be a white vessel passing towards the angle of junction between the jugular vein and the subclavian vein. By very gentle tracing this vessel was found to join the jugular at the angle of junction with the subclavian vein. A chromic acid catgut ligature was then tied round it, about a quarter of an inch from the vein; and it at once seemed to become somewhat distended behind the ligature. After a second thread of catgut had been laid round the vessel at a greater distance from the vein, in order that the vessel might, when necessary, be ligatured again, a pretty considerable opening was made in the vessel, and immediately a white fluid poured out so freely as to fill the wound. Then the other ligature was tied to stop the flow of the chyle; but instead of being tied behind the wound in the vessel, it was accidentally tied over it, so that there was still an escape of the white fluid. A third catgut ligature was therefore put round the vessel, distinctly behind the wound in its walls, and about three-quarters of an inch from the junction with the vein; and this was firmly tied. That the vessel tied was actually the thoracic duct, the chyle which flowed out of it proved.

The dog did not seem to suffer in the least from the operation. It was ordered lean meat that it might not be troubled with unabsorbed fat. It ate its food well, and had regular stools which did not show an unusual quantity of fat. Its weight varied slightly, but at no time showed any decided diminution. On the 4th of March, *i.e.*, a month after the operation, its weight was 6 kilogrammes 10 decagrammes, or 40 decagrammes more than on the day of operation. It was killed on the 11th of March, and then weighed 5 kilogrammes 75 decagrammes.

As in the previous tables, the corpuscles of the blood are enumerated in columns. In another column is the weight of the animal at different dates after the operation.

	Hæmocytæ.	Leucocytes.	Relation of Leucocytes to Hæmocytæ.	Weight.
Before Operation, . . .	8,720,000	14,000	1 : 622·8	5 kilos. 70 decas.
<i>Operation on 2 February.</i>				
3 Feb., 1st day after,	8,590,000	24,000	1 : 316·2	5 kilos. 61 decas.
4 " 2nd "	8,690,000	19,000	1 : 452·1	5 kilos. 45 decas.
5 " 3rd "	8,420,000	17,000	1 : 495·2	5 kilos. 67 decas.
8 " 6th "	7,330,000	14,000	1 : 523·5	5 kilos. 60 decas.
10 " 8th "	7,470,000	12,000	1 : 622·5	5 kilos. 65 decas.
18 " 16th "	7,890,000	10,000	1 : 789	5 kilos. 35 decas.
25 " 23rd "	7,620,000	10,000	1 : 762	5 kilos. 95 decas.
4 March, 30th "	7,570,000	9,000	1 : 841·1	6 kilos. 10 decas.
11 " 37th "	8,630,000	12,000	1 : 719·1	5 kilos. 75 decas.

The examination of the blood-forming organs yielded the following:—

The *spleen* was not remarkable either for size or for softness. If anything, it was rather larger and softer than usual. A scraping, treated as usual, showed very large numbers of "blood-corpuscle-holding cells." These cells, which are pretty constantly found in the spleen and bone-marrow, will be considered later. Only a few nucleated red cells were found in each preparation. Still there were many more than in the spleen of a normal dog, where they either are not found at all or are found only after very diligent search (Bizzozero and others, and confirmed by myself).

Bone-marrow.—The whole length of the shafts of the humerus and femur contained nearly fully reddened marrow, in which a few nucleated red cells were found, most of which were in the earlier stages, some, however, being in the more typical later stages. Numbers of "blood-corpuscle-holding cells" were found in the marrow of all the bones examined. I found more of these cells in the spleen and bone-marrow of this dog than in any other dog. The marrow of the heads of the bones contained less fat than that in the shafts of the bones, and showed numbers of young nucleated red cells and of nucleated red cells intermediate between the very young ones and the more typical, as well as a fair number of the really typical. The marrow of the ribs contained a fair number of nucleated red cells. There was quite as much fat as usual in the red marrow of all the bones, and the marrow in the shafts of the long bones other than the humerus

and femur had its usual fatty appearance. To summarise the naked-eye and microscopic appearances of the marrow: those parts of the bones which always contain red marrow contained marrow richer than usual in nucleated red corpuscles, while in the humerus and femur the usually fatty marrow of the shafts had been replaced by red marrow.

Lymphatic Glands.—In the left axilla there was an unusually large and succulent lymphatic gland, which was redder than usual; and in the right axilla a gland larger than usual, though not so large as that in the left axilla. A scraping from the cut surface of the gland in the left axilla, treated in the usual way with artificial serum and methyl-violet, showed some distinctly nucleated red cells of the later and more typical variety. There were also an unusual number of non-nucleated red corpuscles. In the gland of the right axilla, careful searching gave one or two nucleated red cells in each preparation. The most distinct appearances, however, were found in the glands of the mesentery. These glands were much larger than usual, very soft and succulent, and somewhat red on section. In scrapings from them were large numbers of nucleated red cells, of whose nature there could not be the slightest doubt. Most of these were of the later and more typical variety, and there were comparatively few belonging to the earlier stages. There were also large numbers of non-nucleated red corpuscles. No "blood-corpuscle-holding cells" were found in any of the lymph glands examined. The inguinal glands were very decidedly enlarged.

Thyroid gland of usual size. No evidence of blood-formation could be found in it.

From this case, then, it would appear that the lymph glands even in normal conditions change a certain number of colourless into coloured corpuscles. This is supported not only by the microscopic appearances in the glands, where the nucleated red cells were almost as numerous as the colourless cells, and were more numerous than the nucleated red cells in the marrow of the ribs, but also by the enumeration of the blood-corpuscles during the life of the animal. For the table given shows that a very few days after the operation the red corpuscles showed a decided decrease, and that they remained very distinctly below their original number for fully a month after the operation.

Soon after the fall in the number of red corpuscles, the colourless corpuscles likewise suffered a diminution in their number, the diminution being both absolute and relative, and remaining until the end of the observations on the animal. Between five and six weeks after the operation, the red corpuscles had practically returned to their former number, the red-corpuscle-forming function of the lymphatic glands having been taken up by the marrow of the shafts of the humerus and femur. This, at least, is the only explanation I can find for the transformation of the originally fatty marrow of the shafts of these bones into red marrow.

Very interesting was the condition of the thoracic duct. Its dissection was very easy, as it was rather dilated. The contents, however, which must have been the cause of the dilatation, had disappeared, the duct being empty. The duct had a clear semitransparent pink appearance, which seemed to be due to the colour of its coats. I followed it upwards to its opening into the vein, dissecting very carefully, to avoid destroying any branch. At three-quarters of an inch from the opening into the vein, the distinct tube became suddenly replaced by a white opaque cord. The junction of this apparently obliterated part with the rest of the duct exactly corresponded with the position of the most external of the ligatures; and in this part of the duct one could with perfect distinctness feel three hard nodules, each about the size of a pin's head, in the positions where the three ligatures had been placed. To make certain as to the condition of the duct, I opened it a short distance before the apparent obliteration; and easily passed a fine thread of catgut along it as far as the beginning of the constriction, where it was stopped. And I then tried a horse-hair, but it also failed to pass into the obliterated part of the duct. There can, therefore, be no doubt that the thoracic duct had been tied, and that the result of the tying had been complete obliteration. As to the possible existence of an important branch of the duct, with a corresponding persistence of the circulation of the chyle, it may be stated that I searched very carefully along the whole length of the duct, but could find no branch passing off from it, nor any second duct passing upwards from the receptaculum chyli. I have been unable to find a good description of the lymphatic system in dogs; and from one case, and without careful injection of the thoracic duct, it would, of course, be absurd positively to conclude that the chyle had been altogether prevented from reaching the blood by a collateral channel: still, the facts are in favour of such a conclusion.

Apart from what was found in the lymph glands, the case is extremely interesting from the number of possibilities it suggests. If the passage of the chyle into the blood by the thoracic duct

be prevented, is there any other way by which it can enter the circulation? And if there is no other way, how was it that this dog did not suffer from fat starvation? In answer to this last question, it may be said that dogs can obtain fats from proteids more easily than a human being can, and that in them the conversion of proteids into fats can take place to such an extent as to render the absorption of fat from the intestine superfluous. Amyloids cannot in the case of this dog be supposed to have been a sufficient source of fat, as the animal was fed almost entirely on lean meat. The meat was, however, of course, not *carefully* deprived of its fat.

In this connection, it is important to mention an interesting paper of William Turner's¹ on obstruction of the thoracic duct in the human subject. He in two cases found the thoracic duct entirely obliterated by a thoracic aneurism without emaciation having resulted. He thinks that in all cases where obstruction of the duct comes on gradually collateral channels are established, and that there is no sufficient proof of the statement that obstruction of the duct by an intra-thoracic growth leads to emaciation. He also mentions cases where collateral branches have been found, as well as communications between the lymphatics and veins elsewhere than at the root of the neck. Turner's idea of the gradual establishment of collateral circulation will not apply in my case, because there the obliteration of the duct was sudden. There may, however, previous to the operation, have been unusual communications between the abdominal lymphatics and the venous system. Anyhow, the obliteration of the duct must have caused some obstruction to the flow of lymph, or I should not have found so many developing red cells in the lymph glands.

To return to the light thrown by this case on the function of the lymphatic glands: it seems to me that there is no link wanting in the chain of evidence in favour of the lymphatic glands having and exerting in normal conditions the power of producing red blood-corpuscles. (1) The enumeration of the blood-corpuscles during life showed, for at least a month after the operation, a distinct diminution in the number of red corpuscles, while a diminution in the number of white cor-

¹ Turner, *Ed. Med. Journal*, 1869.

puscles occurred only after the fall in the number of red. (2) Nucleated red corpuscles were found in great numbers in the abdominal lymphatic glands. (3) It was found that the red blood-forming marrow had extended into the shafts of the humerus and femur.

The nucleated red cells found in the lymphatic glands of the spleenless animals point to the same conclusion. And some other recorded observations, when taken together with this case, put, in my opinion, this function of the lymphatic glands entirely beyond the region of doubt.

The first of these observations is the case recorded by Neumann, already alluded to. It will be remembered that he had recourse to the hypothesis that owing to some disease of the vascular walls the red corpuscles had found their way into the terminal lymphatics and lymph sinuses. It seems to me much more likely that he found nucleated and non-nucleated red cells in the lymphatic glands because they were formed there.

Secondly, Weigert¹ found at the *post-mortem* of a case of pernicious anæmia that the lymph glands were large, soft, and red; that their lymph sinuses were filled with lymph uncommonly rich in red blood-corpuscles; and that the large lymph vessels had similar contents. He gives as the explanation of this that first struck him the possibility of there having been some abnormal condition of the vascular walls, which had allowed the red corpuscles to pass out more easily than in normal conditions. But he remarks that, on reading Rindfleisch's paper,² he began to think that it might have been a case of blood-formation in the lymphatic glands, and regrets that he had not examined the glands in the fresh condition with special reference to the presence of nucleated red cells, adding that on hardened preparations he had failed to satisfy himself.

The paper of Rindfleisch quoted by Weigert contains the account of a case where there was general sclerosis of the bones, as the result of rachitis, and where the marrow cavities were practically obliterated. Rindfleisch found the spleen enlarged and soft, and the lymph glands enlarged and resembling the spleen in consistence and appearance. In the lymph glands he found numerous ordinary red cells and numerous nucleated ones. He looked on this as a case of *vicarious* function of the lymphatic glands.

Having thus, on the subject of blood-formation, given all my own experiments except those performed in connection with the

¹ Weigert, "Perniciöse Anämie mit ausgedehnter Lymphangiectasie. Erfüllung der Lymphbahnen mit blutähnlicher Lymphe," *Virchow's Archiv*, Bd. lxxix. p. 390.

² Rindfleisch, *Archiv f. mikrosk. Anat.*, Bd. xvii. (1879).

thyroid gland, and also given what seem to me the more important experiments and opinions of other writers, I shall now proceed to review the facts on which my own conclusions are based. The conclusions themselves are more or less embodied in what has already been said, but a more categorical statement will not be amiss.

In this paper it has already been assumed that the nucleated red cells found in the bone-marrow and elsewhere are the forerunners of the non-nucleated red blood-corpuscles, and it will perhaps seem curious I should only now begin to give my reasons for holding them to be so. In explanation, I would point out, on the one hand, that the function of the blood-forming organs could not have been treated without the assumption, and, on the other hand, that the life-history of the red cells could not have been thoroughly treated without a previous consideration of the blood-forming organs. Under these circumstances, I have chosen simply to indicate at the beginning of the paper what the nucleated red cells are, and then, for the time being, assume that they develop into non-nucleated red cells.

It will here be convenient first to dismiss the hæmatoblasts of Hayem. In the first part of this paper I have pretty clearly indicated my own opinions as to these elements; as also the opinions of Neumann and Bizzozero. It seems to me that Bizzozero finishes the discussion very well, when he expresses the hope that Hayem may "one day see the nucleated red cells in the bone-marrow;" for he thinks that if he does so, and compares them with the nucleated red cells of the embryo, his allegiance to his hæmatoblasts will vanish. And Neumann remarks on Pouchet's explanation of the nucleated red cells found in the bone-marrow (for Pouchet does not deny that they exist), that if Pouchet had compared them with the nucleated red cells of the blood of the embryo "he would not have fallen into the unfortunate fabrication, '*dégénérescence hémoglobinique*,' which leads to the absurd conclusion that the nucleated red cells in the blood of the embryo are nothing else than hæmoglobin-degenerated cells."

Neumann, in his paper in the *Zeitschrift für klin. Medicin*, already mentioned, gives a very good criticism of all the views as to the origin of the non-nucleated red blood-corpuscles, and refuses to accept Schäfer's and Ranvier's view that they may arise endogenously as non-nucleated bodies in the protoplasm of cells, for instance in the subcutaneous tissue of the embryo. And he also refuses to accept the intermediate position taken up by Rollet, viz., that they arise in two ways, either as nucleated daughter-cells or as non-nucleated offspring of pre-existing cells. Rollet thinks with Ranvier that the former mode of development occurs only in the embryo.

Merkel, in Virchow's *Jahresbericht*, says of this paper of Neumann's that its "very well deserved destructive criticism of the views of Hayem, Pouchet, Schäfer, and Ranvier," is worthy of very special attention.

Neumann considers that there is at all periods of life only one way in which non-nucleated red corpuscles originate, viz., as nucleated red cells, like those of the embryo. Rindfleisch, too, in his paper already quoted, says that "we must entirely banish the idea of their arising in any other way than as nucleated red cells, throughout life as well as in the embryo." And Bizzozero is equally certain on the point. In fact, in opposition to Hayem and Pouchet, the opinion that the nucleated red cells in the bone-marrow and other blood-forming organs are the only forerunners of the non-nucleated red corpuscles is almost universal. And it will be evident that my own observations, so far as they go, support it very strongly.

While agreeing that the nucleated red cells are the forerunners of the non-nucleated ones, the different observers on the blood disagree both as to the details of the transition and as to the origin of the nucleated red cells themselves.

To consider first what becomes of the nucleus :—

Kölliker and Neumann say that it disappears from the cell by breaking down, Neumann evidently thinking that in breaking down it becomes absorbed in the general cell substance. Kölliker's observations were made on the nucleated red cells of the embryo, and Neumann's on the nucleated red cells found in the embryonal liver, and in the marrow throughout the whole of life. Neumann gives drawings showing the last remains of the nucleus as a small body of the size of a colourless microcyte, and Kölliker says that it breaks up into two, three, or four fragments.

Rindfleisch, in opposition to Neumann and Kölliker, says that the nucleus, surrounded by a small amount of undifferentiated protoplasm, passes bodily out of the cell. The further history of the nucleus "may," says Rindfleisch, "be a matter for discussion."

Bizzozero, without giving any distinct opinion, is rather in favour of Rindfleisch's view.

From what I have myself seen, I should prefer to support Neumann's view. For I have seen in the bone-marrow nucleated red cells in which there was apparently only a small remnant of the nucleus, and have, like Neumann, entirely failed to find a ring of undifferentiated protoplasm surrounding the nucleus of a *typical* nucleated red cell.

To the view of Obrastzow¹ and Arndt,² viz., that the nucleus in the nucleated red cells has not the character of a real cell nucleus, but is a *post-mortem* appearance, analogous to the precipitation of fibrin, Neumann returns the best answer, when he calls attention to the researches of Fleming on the indirect division of cells. Of the different stages of such indirect division ("Kariokinesis") in the nucleus of a nucleated red cell, elaborate drawings are given by Lavdowsky³ and Bizzozero.⁴

The question of the origin of the nucleated red cells is still more

¹ Obrastzow, *Centralbl. f.d. Med. Wiss.*, 1880, No. 24.

² Arndt, *Virchow's Archiv*, Bd. lxxxiii. p. 18.

³ Lavdowsky, *Virchow's Archiv*, Bd. xcvi. (1884).

⁴ Bizzozero, *Virchow's Archiv*, Bd. xcvi. (1884).

undecided. Neumann, from observations on the bone-marrow, thought that they arose from the leucocytes; but his faith in that idea has evidently been shaken by his observations on the embryonal liver,¹ where he finds that the red cells arise from nuclei which appear in the protoplasm of large cells like the proper cells of the liver; that these nuclei first come to possess a very thin ring of hæmoglobin-coloured perinuclear substance; that this thin ring gradually increases in breadth until typical nucleated red cells are produced; and that these nucleated red cells then pass out of the mother-cell, to multiply by division in the liver and in the circulating blood. The "mother-cells" were first discovered by Gerlach,² and were called by him "blood-corpuscle-holding cells," because he thought they contained young red blood-corpuscles. Gerlach,³ however, changed his opinion of them when Kölliker⁴ and Ecker⁵ pointed out that they did not contain young red blood-corpuscles, but were probably cells which had taken up extravasated blood-corpuscles.

In spite of the very strong testimony of such an authority on the blood as Neumann, I think that the view taken by Kölliker and Ecker, or a modification of it, will turn out to be the right one; and that even the nucleated red cells found by Neumann in the "blood-corpuscle-holding cells" had been taken up from the tissues. I shall return to these "blood-corpuscle-holding cells" when I consider similar cells found in the spleen and bone-marrow. In his last work on the blood, Neumann says: "As to the origin of the early stages of the nucleated red blood-corpuscles, which, as is known, is still very little understood, I need here say no more." Not only Neumann, but also Rindfleisch, Bizzozero, and many others, affirm that the nucleated red cells increase in number by indirect division; and Bizzozero, in his last paper,⁶ states that they increase only by indirect division, and that all the other views which have been advanced as to their origin (for example from the leucocytes) are mere hypotheses. In making this statement, however, which he applies to all classes of vertebrates, Bizzozero seems to forget that he very strongly incriminates himself. For in his paper on the development of blood-corpuscles in birds,⁷ he not only speaks of the nucleated red cells as arising from the colourless cells of the marrow, but gives diagrams of the different steps of development, and says that the colourless cells pass out of the marrow pulp into the veins of the marrow before assuming hæmoglobin. In his last paper, he urges that the nucleated red cells cannot arise from the white cells, because they are never found in the lymph glands or lymph follicles, where white corpuscles are most numerous. This objection, however, as my experiments have already shown, may be got over.

¹ Neumann, *Archiv der Heilkunde*, Bd. xv.

² Gerlach, *Zeitschr. für rat. Med.*, vii. (1849), p. 79.

³ Gerlach, *Handbuch der Gewebelehre*, 2. Aufl. (1860), p. 56, 58.

⁴ Kölliker, *Zeitschr. für wiss. Zool.*, ii. (1850), p. 117.

⁵ Ecker, *Zeitschr. für wiss. Zool.*, ii. (1850), p. 276.

⁶ Bizzozero, *Virchow's Archiv*, Bd. xcv. (1884).

⁷ Bizzozero, *Moleschott's Untersuchungen*, Bd. xii.

As will have been seen from my descriptions of the appearances in the bone-marrow and other blood-forming organs of the animals on which I experimented, I have come to definite views as to the origin and development of the nucleated red cells. And it will also have been noticed that my conclusions agree with those of Kölliker and Fahrner¹ and others, who hold that the nucleated red cells are derived from the colourless corpuscles.

My description of the origin of the nucleated coloured cells in the marrow corresponds almost exactly with that given by Malassez;² but as to their further history differs very much from that of Malassez, and agrees with that given by Neumann and Bizzozero.

Malassez says:—"They arise in the bone-marrow from cells which have a large nucleus which nearly fills the whole cell. The next stage is shown by the presence of a trace of hæmoglobin in the cell, the cell still having a large nucleus, which is granular, and is not so strongly coloured by staining agents as the nucleus of the earlier stages of the cells. The protoplasm becomes more and more hyaline, the hæmoglobin-stained contents at the same time increasing in quantity, and the nucleus becoming still less easily affected by staining agents." The last stage in this process he calls that of "*cellules hémoglobiques*."

Up to this point, i.e., to the production of the "*cellules hémoglobiques*," I can quite agree with Malassez's description; but here my description diverges very much from it, and agrees with those of Neumann, Bizzozero, and others.

According to Malassez, buds appear on the side of his hæmoglobin-coloured cell, in some animals (young goat) many buds appearing, in other animals (rabbit, calf, cat, and ox) only one bud being evident; and these buds, according to him, enlarge and become non-nucleated red blood-corpuscles, the cell remaining and enlarging to produce more buds.

Bizzozero's explanation of the presence of these buds is, that as he could never see them in preparations treated with neutral fluids, therefore they must have been produced by the action of the osmic acid with which Malassez prepared his specimens. And this explanation receives great support when we remember that by means of reagents, such as tannic acid, buds can be produced on the ordinary red blood-corpuscles.

I do not at all deny that one of the methods by which the nucleated red cells increase in number is indirect division. That they can and do increase in that manner, has been put beyond all doubt by the researches of Bizzozero, Neumann, and others. I do, however, say that there is also a fresh production of the nucleated red cells throughout the whole of life; and that in the blood-forming organs of the animals observed by me there were not a sufficient number of dividing nucleated red cells present to account for the numerous nucleated red cells found, while there were always numerous examples

¹ Kölliker, *Zeitschr. für rat. Med.*, Bd. iv. (1845), p. 112.

² Malassez, *Gaz. méd. de Paris*, 1881, No. 49.

of the intermediate stages between the colourless marrow cells and nucleated red cells.

To describe the transition stages more particularly:—

The condition of one of the colourless marrow cells before beginning to assume hæmoglobin is that of a cell of from 10 to 12, or sometimes even 14, *micros.* in diameter, with a relatively very large nucleus, almost filling the cell, and finely-granular perinuclear protoplasm (fig. 1, *a*). The first appearance of hæmoglobin in this cell is in the form of a thin ring at the periphery of the cell; and between this ring and the nucleus a small amount of the finely-granular perinuclear protoplasm can often still be observed. More frequently, however, the band of hæmoglobin-tinted substance seems to fill the whole space between the cell-envelope and the nucleus, and the perinuclear substance has the same clear appearance as the substance of the non-nucleated red corpuscles (fig. 1, *b*). As this hæmoglobin-tinted perinuclear substance increases in amount, the nucleus appears to become smaller and to retreat towards the centre of the cell, the cell as a whole at the same time becoming smaller (fig. 1, *c*).

I have, in my preparations, been able to see all stages of transition, between the comparatively large young nucleated red cells and the much smaller typical nucleated red cell, measuring about 9 *micros.* in diameter, where the nucleus, too, is much smaller, and the perinuclear coloured substance is much broader (fig. 1, *d*). My conception has been, that previous to the assumption of hæmoglobin the nucleus of the colourless marrow cells enlarges and comes to occupy almost the entire cell, and that under the influence of the nucleus the peripheral part of the cell assumes hæmoglobin, the nucleus at the same time becoming smaller. That the nucleus enlarges previous to the assumption of hæmoglobin, I infer from the fact that there are in the bone-marrow and other blood-forming organs many large colourless cells which contain nuclei not so very large as compared with the cells and yet in other respects resemble the cells of fig. 1, *a*, supposed by me to be marrow cells in the condition immediately preceding the assumption of hæmoglobin. These large colourless cells, with nuclei not so disproportionately large, are the

cells in the blood-forming organs that seem to me to divide most actively. In particular, they seem to divide much more actively than the nucleated red cells, of whose division, however, I have seen indubitable examples.

It would accordingly appear that the nucleus takes an active part in enabling the cell to assume hæmoglobin, and then, as being of no further use, disappears from the cell; and my belief in this function of the nucleus is one of my reasons for thinking it unlikely that the non-nucleated red corpuscles, while circulating in the blood, possess different amounts of hæmoglobin. For I cannot think that without the presence of a nucleus the red corpuscles have it in their power to add to the hæmoglobin they contain. Perhaps, however, it would be premature to deny that the amount of hæmoglobin assumed under the influence of the nuclei may in some diseases be abnormally small.

I could not obtain evidence of small nucleated red cells increasing in size: the small nucleated red cells which were seen in my preparations could, I thought, always be accounted for by the effect of the diluting fluid. The young nucleated red cells show a still greater tendency to crenate and contract into small globular bodies than the non-nucleated red cells do. Those nucleated red cells which were dividing were always large enough to produce two daughter-cells of nearly the same size as the ordinary red cells. The developing red cells in the lymph glands were in the younger stages not so large as those found in the marrow, but in other respects the development seemed to be the same. In the spleen, the development of red cells is the same as it is in the bone-marrow.

Those white cells which are transformed into nucleated red cells in the bone-marrow are not necessarily all produced there: it may be that many of them are produced in the lymphatic glands, and carried to the bone-marrow, there to enlarge and pass through the various stages of the transformation.

The white blood-corpuscles, whether produced in the lymph-glands, spleen, or bone-marrow, seem to me to be the forerunners of the nucleated red blood-corpuscles:—

(1) Because those cells in the bone-marrow which belong to the stage in the development of the nucleated red cells previous to the appearance of hæmoglobin are exactly similar to enlarged

white corpuscles, while the bone-marrow contains besides such cells also many white corpuscles of ordinary size. (2) Because in the lymphatic glands nucleated red cells were found which had evidently been developed there, and also white cells with peculiarly clear perinuclear substance, which looked as if they needed nothing but hæmoglobin to convert them into nucleated red cells. (3) Because when the lymph is prevented from entering the blood the number of red corpuscles in the blood falls. (4) Because after excision of the spleen, which is an organ for forming *white* blood corpuscles, the white corpuscles in the blood on the one hand increase in number while the red corpuscles decrease, and on the other hand may sink even below their original number as the red corpuscles rise again to theirs. (5) Because a leucocyte is typically an embryonic cell capable of further differentiation.

I entirely agree with Neumann, Rindfleisch, and Bizzozero, in thinking that the only forerunners of the non-nucleated red corpuscles, during the whole of extra-uterine life as well as during intra-uterine life, are the nucleated red cells found in the blood-forming organs. Now that it can be shown that these cells exist in the blood-forming organs throughout the whole of life, there is really no necessity for having recourse to microcytes, and endogenous cell-formation, in order to explain the blood-forming process. For why should the origin of the blood-corpuscles in extra-uterine life be different from their origin in intra-uterine life? And, on the other hand, it has been abundantly shown that the nucleated red cells increase in number in the blood-forming organs in direct proportion to the necessity for the formation of blood, and accordingly increase most when the blood is being most actively regenerated. So that we cannot have any stronger proof that they are young red blood-corpuscles.

These cells, then, being accepted as young red blood-corpuscles, the question arises, "Which is the organ most active in their formation in extra-uterine life?" In answering it, I must, as the result of my own experiments, agree with Neumann and Bizzozero that the *bone-marrow* is the most active producer of red blood-corpuscles during extra-uterine life: that is, in the generality of animals; Bizzozero having found that in tailed

amphibians and in fishes the chief blood-forming organ is the spleen.

From personal experience, I can, of course, speak only of the blood-forming organs of dogs. In these animals, the red marrow appeared to be the chief organ; though the spleen, too, at any rate within the first year of extra-uterine life, produces red blood-corpuscles, and does so even under normal conditions. I should say that the spleen probably throughout life forms a certain number of red blood-corpuscles.

Experiment V., where the dog was at least two years old, gave the strongest possible evidence in favour of Bizzozero's view that the spleen actively produces red corpuscles when the blood-forming capabilities of an animal are called into play by loss of blood.

As to the function of the lymphatic glands in the formation of red blood-corpuscles, Experiment VIII. proved—as it seems to me, conclusively—that the lymphatic glands do, during the whole of extra-uterine life, take part in the formation of the red blood-corpuscles. But, from the cases of excision of the spleen, it appears that their activity in this respect is at any rate less than that of the bone-marrow; and I think it very probable that it is also less than that of the spleen.

As to how the young red blood-corpuscles formed in the bone-marrow pass into the circulation, there are two opinions—that of Rindfleisch, which is adopted by Neumann, and that of Bizzozero. Rindfleisch supports the view which Hoyer¹ and Rüdinger² took in 1869, viz., that the greater part of the capillary system in the bone-marrow possesses no special wall, but that the thin-walled arteries open into tunnels in the marrow-substance (i.e., into the interstices of the marrow-pulp), and that the veins take origin from these tunnels. He argues that it would be quite superfluous for the capillaries of the marrow to possess walls, because the circulation in the marrow must be a restricted one, from the hard bony surroundings making the inflow and outflow of blood always correspond. Bizzozero,³ on the other hand, considers that the capillaries of the marrow are real capillaries, and have distinct thin walls, and that the veins arise as very wide channels, also with very thin walls. He further considers, or rather considered,⁴ that the colourless marrow-

¹ Hoyer, *Centralbl. f. d. med. Wiss.*, 1869.

² Rüdinger, *Centralbl. f. d. med. Wiss.*, 1869.

³ Bizzozero, *Morgagni*, 1869.

⁴ Bizzozero, *Moleschott's Untersuchungen*, Bd. xii.

cells, before assuming hæmoglobin, pass through the thin walls of the veins into their lumen, there to assume hæmoglobin; and that they never contain hæmoglobin until they enter the veins, no hæmoglobin-containing cells being visible outside the vessels. As, however, in the same paper, he talks of its being a doubtful question whether the blood-channels in the *spleen* have or have not distinct walls, we may take his view of the condition of the circulation in the bone-marrow with some reserve. The question is, of course, a very difficult one to settle; for it is difficult to get the marrow so hardened as to allow of satisfactory sections being made. I think it, however, more likely that Rindfleisch's opinion will turn out the correct one.

A word must be said about the so-called "blood-corpuscle-holding cells":—

As has already been mentioned, these cells were discovered, in the liver of the embryo, by Gerlach, and were at first thought by him to contain developing red blood-corpuscles. Gerlach, however, afterwards gave up this view, and accepted that of Kölliker and Ecker, who considered them to be cells which had taken up extravasated blood-corpuscles. Neumann rediscovered these cells, and recognised them to be the same as those described by Gerlach, but considered Gerlach's original opinion about them to be correct. Gerlach's original opinion and description were as follows:¹—He said he found "coloured blood-corpuscles in large numbers lying as cell-contents inside large colourless cells;" and said, further, that "these enclosed bubble-like, reddish-yellow nuclei (*viz.*, the 'coloured blood-corpuscles'), become free, and, perhaps by the formation of an envelope (*Hülle*) and the sharing of the colouring matter with this envelope, become transformed into coloured blood-corpuscles." This description of Gerlach's exactly applies to "blood-corpuscle-holding cells" which I have found in the spleen and bone-marrow, and supports the view taken by Kölliker and Ecker. Neumann objects to this view chiefly because he found *nucleated* red corpuscles in these large mother-cells and found, as he thought, stages of transition between "free nuclei" contained in the cells (but differing from the proper nucleus of the cell) and the typical nucleated red corpuscles. To turn Neumann's explanation of Hayem's hæmatoblasts against himself, one may ask, Is it not possible that in embryonal life some of the *nucleated* red corpuscles are, as easily as the *non-nucleated* ones, extravasated and taken up by the large cells, and that the transition-stages in the "development" of the nucleated red corpuscles observed by Neumann in "mother-cells" are simply stages of breaking-down of such corpuscles in cells which had taken them up?

I have no personal knowledge of the "blood-corpuscle-holding cells" in the embryonal liver, but can speak of similar cells in the spleen and bone-marrow—cells whose function seems to be to take up breaking-down red blood-corpuscles, complete their break-

¹ Gerlach, *Zeitschrift für rationelle Medizin*, vii. (1849), p. 79.

ing-down, and perhaps in some way prepare their hæmoglobin for being again made use of. In the accompanying drawings my reasons for supposing this function will be seen (fig. 2). The cells vary from about 8 or 10 *micros.* to perhaps 40 *micros.* in diameter. The nucleus is, as a rule, pushed to one side, and often flattened, like the nucleus of a fat cell. In some cells, however, I was, like Neumann, unable to distinguish a nucleus.

The peculiar contents of these cells are well described in Gerlach's words, as "bubble-like reddish-yellow nuclei"; except that they cannot be called "nuclei," having, in fact, none of the characters of nuclei. They are perfectly clear, show no granulation, and are darkly coloured with hæmoglobin. Of course, Gerlach's after-admission that they are breaking-down coloured corpuscles shows that he gave up the idea of their being nuclei.

These "blood-corpuscle-holding cells" contain, generally according to their size, one or several "bubble-like reddish-yellow" bodies, which vary very markedly in size, and vary in colour directly with their size. In some of the cells there can be seen, in the centre, a round or irregular coloured body, often many times larger than a normal red corpuscle; which at first may appear single, but when carefully focussed is seen to be composed of a number of smaller bodies closely packed together (fig. 2, *b*). As a rule, around this darkly-coloured mass there are many small straw-coloured fragments, which have exactly the same appearance as the fragments of a broken-down red corpuscle. The general finely granular protoplasm of the cell has, as a rule, a faint hæmoglobin tint. Different examples of these cells are shown in fig. 2.

It would appear that under the influence of these cells the hæmoglobin-substance of the broken-down red corpuscles is fused into a common mass; but whether their function is to prepare hæmoglobin to be again made use of as hæmoglobin or to prepare it for being carried to the liver to be there made use of, it would be difficult to say.

Before giving a summary of my conclusions, I should like again to draw attention to the excellent advice of Neumann and Bizzozero, who urge that the substance of the blood-forming organs should, like the blood itself, always be examined fresh, and either undiluted or diluted with *neutral* fluids.

The conclusions are:—

1. Nucleated red cells, derived from white corpuscles and colourless marrow cells, are the only forerunners of the non-nucleated red blood-corpuscle, throughout the whole of life.
2. The transformation of the colourless cells into nucleated red cells takes place in the bone-marrow, spleen, and lymphatic glands.
3. The colourless cells and the nucleated red cells multiply in the blood-forming organs by division.
4. The red bone-marrow plays the most important part in the production of red blood-corpuscles during extra-uterine life.
5. After the production of anæmia, some of the fatty marrow becomes red marrow, and joins in the formation of red blood-corpuscles.
6. The blood-forming action of the spleen is in extra-uterine life a subordinate one, but when the reserve blood-forming capabilities of an animal are called on its activity is greatly increased.
7. After excision of the spleen, a portion of the formerly fatty marrow becomes red marrow, and the lymphatic glands increase their activity as regards the production of red blood-corpuscles.
8. After excision of the spleen, the red corpuscles in the blood decrease in number, and there is a consequent increase in the number of white corpuscles. The red corpuscles return to their normal number within six months, after which there may be a decrease in the number of white corpuscles.
9. The chief function of the lymphatic glands is the production of white corpuscles, but they also, even in normal conditions, produce a certain number of red corpuscles. Their activity in the latter respect increases with the necessity for the production of red corpuscles.
10. The spleen and bone-marrow, and possibly also the lymphatic glands, contain cells whose function appears to be to break down red blood-corpuscles.¹

¹ With reference to Dr Gibson's thesis, Dr Creighton has called the Editors' attention to a paper by himself (Dr C.), "Illustrations of the Pathology of Sarcoma," published in 1880, in the April number of this *Journal*, claiming that it contains an important contribution to the study of blood-formation, and that he has developed his hæmatoblastic doctrine further in the article "Pathology" in the *Encyclopædia Britannica*. As Dr Gibson sailed for Queensland some months ago, it has not been possible to bring Dr Creighton's papers under his notice, but the Editors take this opportunity of referring to them.

EXPLANATION OF PLATE XIV.

Fig. 1. *a*, Colourless marrow-cells, that is, marrow-cells before the appearance of hæmoglobin in them. *b*, First appearance of hæmoglobin in marrow-cells. *c*, A later stage of the marrow-cells. *d*, Typical nucleated red cell. *e*, Probably shows the remains of a nucleus in a red cell. *f*, Ordinary non-nucleated red corpuscles, to serve as a scale.

Fig. 2. *a*, Small "blood-corpuscle-holding cell," containing one pretty large "bubble-like reddish-yellow" body. *b*, Large blood-corpuscle-holding cell, containing many broken-down and partially fused red corpuscles (bubble-like reddish-yellow bodies). *c*, The same as *b*, but with fragments more completely fused together in centre. Many small isolated fragments of red corpuscles in the periphery of the cell. *d*, Shows small nucleus (unstained), pushed into a corner. Various bubble-like bodies: some very faintly hæmoglobin-tinted, one very deeply tinted. *e*, Large "blood-corpuscle-holding cell," with nucleus (unstained) pushed to one side and flattened. Many bubble-like bodies. The larger the bodies, the more darkly are they tinted with hæmoglobin. *f* and *g*, Other examples of "blood-corpuscle-holding cells."

(To be completed in the next number.)

INVESTIGATIONS IN THE RELATION BETWEEN CONVERGENCE AND ACCOMMODATION OF THE EYES. By ERNEST E. MADDOX, M.B. Edin., *Syme Surgical Fellow in the University of Edinburgh*.¹

I. *Introductory Sketch.*

WHY, if we see separately with *each* eye, do we not see *double* when both are used? This problem has taxed the ingenuity of many busy minds in past ages, and its history is by no means one of uniform progress.

Euclid, two or three centuries B.C., had advanced so far beyond some at a far later date as to recognise that both eyes were employed in unison, and that their dissimilar pictures were in some way united. Galen surmised that the union of the optic nerves at the commissure supplied a clue. Both he and Herophilus assumed that the two nerves were there united by mysterious pores; doubtless to permit the free passage and intercourse of the little spirits of both sides, whose remarkable unanimity in fitting the pictures together was evidenced by single vision. Later on Gassendus, Tacquet, and Joan Baptista Porta, the inventor of the camera obscura, escaped the difficulty altogether by assuming that one eye only at a time was engaged in vision.

In 1613, Francis Aguillon (Aguilonius), a learned Jesuit, called in the aid of what he termed a "common sense," which "imparts its aid equally to each eye, exerting its own power equally in the same manner as the eyes are converged by means of their optical axes." This was an advance, for the two pictures, we may truly say, are mentally united by a "common sense,"² of the real nature of which we probably know little more than Aguilonius, though we may notice more of its effects.

Dr Briggs appears to have been the first to have suggested "corresponding" or "identical" points in the two retinæ, that is, that each point on the inner side of one retina has a corresponding point on the outer side of the other, so that when images are thrown by an object upon these identical points, they are mentally united. This was a great advance, though the theory of "identical points in the *field of vision*" is now considered more correct. But he explained it in a

¹ The original of this memoir was the successful essay submitted in competition for the Syme Surgical Fellowship in April 1884. Before publication it has been revised and enlarged.

² It is now located in a theoretical "fusion centre."

curious way, by ascribing to *each fibre* of the optic nerve a different degree of tension, like the strings of a violin or piano, each vibrating in unison with its own retinal area,—“a tension,” argued Porterfield, “impossible in the soft and pulpy structure of the nerve fibres.”

From the fact that “in animals which look the same way with both eyes, the optic nerves meet before they enter the brain, while this union does not occur in those which do not, such as fishes and the chameleon,” Sir Isaac Newton suggested an arrangement of the optic fibres at the commissure, which exactly tallies with that now generally received—“the fibres on the right side of both (optick) nerves uniting there at the commissure, and, after union, going thence into the brain in the nerve which is on the right side of the head, and the fibres on the left side of both nerves uniting in the same place, and, after union, going into the brain in the nerve which is on the left side of the head.” I quote from the 13th Query at the end of his “Treatise on Opticks” (1718), the more remarkable because it was the belief of anatomists, like Vesalius, that no decussation occurred at the commissure, and that it consisted of fibrous tissue.

Dr William Porterfield of Edinburgh is believed to have first enunciated the correct, though still very partial theory of binocular vision. In his “Treatise on the Eye” (1759)¹ he showed that when the eyes are accommodated for any object their two visual axes are also exactly converged upon the same point, and “since each eye possesses the power, either intuitively or by acquisition, of localising points in space, the object *must* appear single, it being impossible for us to conceive two objects existing in the same place at the same time.

Single binocular vision therefore requires a *perfect concert* between the efforts of accommodation and convergence. The former secures *distinct* vision; the latter *single* vision.

Accommodation affects the *nature* of the images thrown on the retinae; convergence affects their *position* on the retinae, so that they still fall on the same portions whether the object looked at is near or distant. If distant, both accommodation and convergence are *nil*. With every approach or recession of the object, they increase or decrease simultaneously. The two efforts are not only associated in their daily exercise, but the nervous centres which govern them are linked in the brain by strong nervous ties, so that the slightest action of one affects the other. This is shown by Donders' experiments, for, though they demonstrate that the desire for single vision has power to *overcome* the nervous ties within limits, when lenses or prisms are used, yet they show also that the slightest alteration in

¹ To which I am indebted for most of what precedes.

convergence shifts both limits of the possible play of accommodation in the same direction.

Further evidence was given by Dr Loring, who, while looking at an object through concave lenses, *reduced* the desire for fusion by placing coloured glass before one eye, and thus produced diplopia. The distance between the two images varied with the strength of the lenses worn, showing that "for every degree of tension of the ciliary muscle there is a corresponding degree of tension of the interni."

Convergence, like accommodation, is brought about by a *single* effort. Hering's theory may well be mentioned here, since it receives striking and repeated confirmation in the following pages. It is that "each eye is supplied by two innervations—one directed to the turning of *both* eyes to the right or left, the other to turning both eyes inward or outward." "Both eyes are used in the service of the sense of sight as a single organ consisting of two separate limbs."

The movements of both eyes to the right or left may for convenience be called "ranging" movements. They depend on two distinct mechanisms, which have no known connection with each other. Of these, one supplies the external rectus of the right eye and the internal rectus of the left, and turns both eyes to the right; the other supplies the remaining lateral recti, and turns both eyes to the left. When both ranging centres evolve an equal quantity of nervous energy the result is simply increased tension of all four lateral recti, since each internus antagonises its fellow externus. If one centre predominates, both eyes are deviated to the right or left as the case may be.¹ Stimulation of Ferrier's area 12 in the frontal lobe causes among other movements turning of both eyes to the opposite side. It is clear, therefore, that "*convergence*" or intersection of the visual axes is not provided for by this innervation. It is brought about by a separate and superadded effort, and is provided for by a mechanism which affects both eyes equally.

¹ In the notes Adamuk finds a common centre for both eyes, stimulation of the right side producing movements of both eyes to the left, of the left side movements to the right, while stimulation in the middle line behind causes a downward movement of both eyes with convergence of the axis, and in the front an upward movement with return to parallelism, both accompanied by the naturally associated movements of the pupil.—*Michael Foster*.

When an object is viewed in the mesial plane the effort of convergence causes the two visual axes to intersect at the point of fixation, and no effort is needed on the part of either ranging centre. But if the point of fixation is carried ever so little to the right or left of the mesial plane, convergence must be supplemented by an effort of one of the ranging centres to carry the point of intersection into the required plane.

Is the central connection between the efforts of convergence and accommodation complete? Though the nervous association can be partly overcome when necessary by prisms or lenses, it does not follow that it should be naturally incomplete, and it has generally been supposed that a normal eye when excluded from vision would remain *in statu quo*. Consistently with this, since the demand for accommodation is relatively greater in a hypermetrope and less in a myope than in normal eyes, it has been supposed that under the same conditions the eye of every myope would deviate outwards, and that of every hypermetrope inwards. We shall find this is far from being the case.

II. *The Blind-spot Method of employing the "Visual Camera."*

The object of this method is to ascertain the behaviour of an eye placed subjectively in the dark when the other eye is employed in vision. The blind spot, or "punctum cæcum," is a nearly circular gap in the field of vision of each eye discovered by Mariotte, and shown by Donders to be due to the fact that the entire surface of the "optic disc" (the extremity of the optic nerve at its entrance into the eye) is wholly insensible to light. When one eye is closed, therefore, there is an area in the outer part of the field of vision of the other entirely devoid of visual impressions, and large enough, according to Helmholtz, for eleven full moons to stand in a row in it (*Handbuch der Physiologik Optik*, 1867). The method of its employment for our purpose is illustrated in fig. 1, which represents a dark box or camera of a flattened pyramidal shape, measuring about a foot from side to side and nine inches from before backwards.¹ The narrow end contains two visual apertures, pierced through slides (*a, a*), which permit their mutual distance to be regulated as the eyes of different observers require.

¹ To be obtained from Messrs Pickard & Curry, 7, Gt. Portland St., London.

The curved border of the box is built up of two arcs (d, d) united by a straight line nearly $2\frac{1}{2}$ inches long, and therefore equal to the average distance between the centres of the two eyes, while each arc is part of a circle drawn from the centre of motion¹ of the eye of the same side. This end of the box is provided with three luminous points, one fixed (e) and two

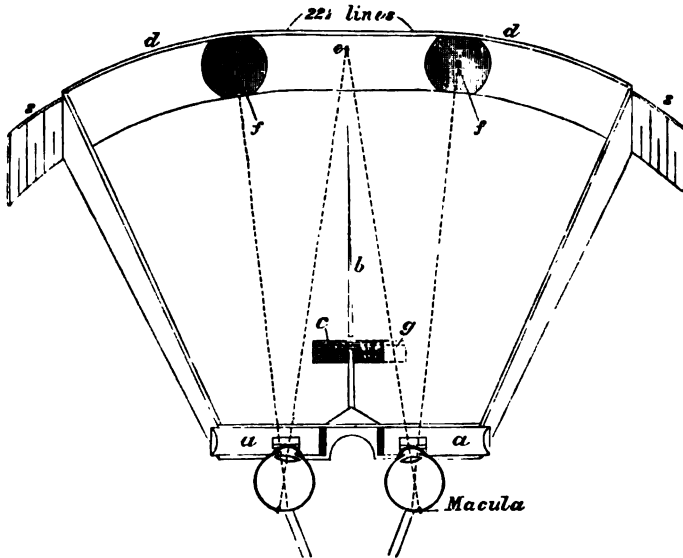


FIG. 1.—View of the visual camera with the roof removed.

(Erratum.—The dotted lines should cross *in* the crystalline lens instead of behind it; $22\frac{1}{2}$ lines should be $28\frac{1}{2}$ lines.)

movable (f, f). They are tiny apertures, which become luminous when the box is held up to the light. The central one (e) is stationary, and since it is used as the point of fixation, should be provided with a piece of ground glass, a letter, or cross wires, to fix attention.² The lateral points (f, f) are preferably coloured,

¹ This point is about 13 mm. (Donders) behind the anterior surface of the cornea. Nearly half an inch is allowed for the distance of the cornea from the visual apertures, so that since the box is 9.2 inches from before backwards, points on its *further* border are 10 inches from the *dioptric* centres, and therefore when looked at require 4 dioptries of accommodation to be in exercise. A dioptre is the chosen unit of refractive power; it is that possessed by a spherical lens of the focal length of a metre (nearly 40 inches). *Four* such lenses would represent the *increase* in the refractive power of the crystalline lens required to focus on the retina distinct images of points 10 inches distant.

² In default of these it suffices to moisten a piece of printed paper and apply it to the outside of the aperture.

and are pierced through brass slides (*s, s*) which travel in grooves, so that each aperture can be moved at pleasure along its own half of the curved end independently of the other and of the central one, and without the admission of any additional light. This is brought about by a system of long slits so cut in the brasswork that the two slides and the side of the box against which they are apposed mutually overlap each other's slits, and yet permit the points of light to be seen through. A graduated scale of degrees (made by taking as a radius the centre of the eye of the same side) is attached to the outer surface of the arcs, and indicates the angular interval between each of the movable points and the central one.

The camera is nearly divided into two lateral compartments by a median vertical partition (*b*), which runs forward to within an inch or two of the central luminous point. It is interrupted by a small cross-piece of wood called the "stop" or "obstructive" (*c*), which is let in through a slit in the roof, and can be made to travel shortly from side to side so as to intercept at pleasure the view of the central point (*e*) by either the right or left eye. This is shown to the right in dotted outline (*g*), but the central point (*e*) is perfectly visible by *both* eyes, so long as the "stop" is in the middle of its slit, as represented by the *shaded* portions of the figure (*c*).

Since the optic nerve enters the eye to the *inner* side of the visual axis, and since all projections are reversed in position, there is an area on each side of the curved end of the box (represented by a shaded circle) which corresponds to the projection of the blind spot of the eye of the same side, and which may be called the "blind area." Each is about an inch in diameter at this distance from the eye. It may be observed that vision of the *movable* points is *always* monocular, since the median partition (*b*) cuts off the view of each from the opposite eye; whereas vision of the *central* point is either monocular or binocular at pleasure according to the position of the "stop," the motion of which is too short to interfere with the view of either of the *movable* apertures, though wide enough to interfere (when desired) with the view of the central one by either eye.

EXP. 1.—As a preliminary, push the *left* brass slide inwards until the point it bears is overlapped by the brass work and thus

disposed of. It is not needed in the observation. Put the stop in the *middle* of its slit, and leave the *right* movable point within the usual limits of the right blind area. Now let the subject of the experiment hold the camera up to the light and look steadily with both eyes at the central fixation point. The right luminous point, being in the blind area, is then out of sight *so long as* the stop is in the middle. Now push the stop to the right, and it will be found that though the observer does not know what has happened, and still thinks he sees as before with both eyes, yet in most cases, after the lapse of a moment or two, the hitherto hidden point springs into view, showing that the eye has deviated from its former position, and has allowed the image of the luminous point to fall on a sensitive portion of the retina, as in fig. 2.

The only effect of which the observer is conscious when the stop is pushed to the right is that the fixation aperture appears less bright,¹ yet by so doing the right eye is excluded from vision entirely, and placed subjectively in the dark, since of the two apertures the fixation one is cut off by the stop and the other throws its image on the blind spot where it produces no impression. He is aware neither of the exclusion of the eye nor of its deviation.

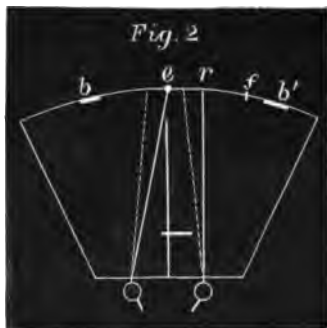


FIG. 2.—The vision of the central aperture (*c*) being cut off by the stop from the right eye, its axis has deviated from *c* to *r*, and its blind area (*b'*) has moved to exactly the same extent, so that it no longer conceals the point of light (*f*). The *left* blind area (*b*) does not move, showing that only one eye deviates.

If now, *after* the eye has deviated, the right brass slide is drawn outwards, the movable point it bears again becomes lost to view in the blind area, showing that the deviation was *outwards*. Its exact extent may be measured in degrees by reading off from the graduated scale, the position of the inner border of the blind area *before* and *after* the eye has deviated, that is, *first* with the stop in the middle and *then* to the right. The difference between the two records gives the angular deviation of the visual axis. In my own eyes it is about 5° as a rule, though it varies from 3° to 7° or even 8°, according to the time of day, the temporary comparative anæmia or congestion of the brain, the previous occupation of the eyes, and doubtless many other conditions. It appears to be greater in the morning than in the evening, and less after much reading, or with congestion of the eyes from close work or hot rooms. That there should be any *outward* deviation at all in my case was an unexpected result, owing to the presence of at least 2 D of hypermetropia, for it has hitherto been supposed that when excluded from vision a hyperme-

¹ The central aperture sometimes also appears to move slowly to the right, but this is not generally noticed unless attention is called to the fact.

tropic one deviated *inwards*.¹ I believe, however, that a great many eyes with minor degrees of hypermetropia would be found to deviate outwards, and that if this were duly estimated some of those difficult cases might be more readily relieved which are so sensitive to any disturbance of the requisite relation between convergence and accommodation.

The psychical factor furnishes an occasional difficulty in the observations when there is a constant *expectation* of seeing the hidden point appear. It may be guarded against by registering the position of the

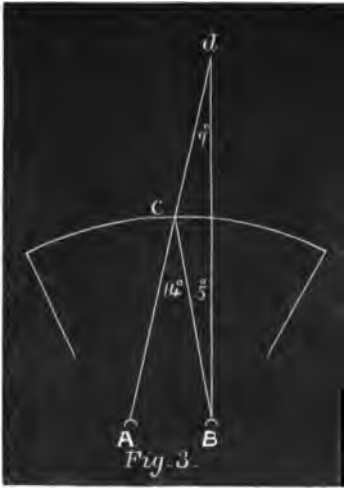


FIG. 3.—AcB was the optic angle before the right eye deviated. AdB is the optic angle *after* deviation; it is less than before, by the angle of deviation cBd.

outer as well as the inner border of the blind area in both records, which thus mutually correct each other, since the same mental effort which might prematurely bring the hidden point into view when one border is being tested would do the very reverse when the other is under trial. Moreover, if the recorded breadth of the blind area be found equal in the two observations, before the deviation and after it, the coincidence is reassuring as to the exactness of the records. Variations in the shape and size of the "disc" in no wise affect the experiments, since the same definite point in each border is taken as the index of deviation. The shape of the curved end of the box is such that each movable aperture in any part of its range still throws a tiny and *distinct* image upon the retina instead of a diffused one; for,

as Donders has said, "in the emmetropic eye the whole curvature of the retina lies in the focal surface of the dioptric system." The image is about $\frac{1}{7}$ th the size of the aperture, so that the latter being half a line wide its image is about $\frac{1}{100}$ th of an inch in width.

¹ I am indebted to Mr Brudenell Carter's "Defects of Vision" for the fact that Hansen has recorded a few instances of "central defect," though Mr Carter had not identified them (1877, p. 141), and says: "In every case of myopia the tendency of the visual axes would be towards divergence, and in every case of hypermetropia the tendency would be towards convergence as soon as the control exercised by the demand for fusion was withdrawn" (p. 138). To Hansen then belongs the first notification of the fact that in "a few persons" an excluded eye diverges with the ordinary tests at reading distance. I think, however, the camera will show that instead of being a rare exception, this is the *normal* condition, though not the invariable one. Doubtless Hansen's cases were, in one sense, *really exceptions* to the normal, in that the degree of deviation was large enough to be detected by the ordinary methods.

It may be stated as a simple geometrical necessity¹ that the angular deviation of either eye alters the "optic angle" (or "angle of convergence" contained between the *two* visual axes), by the *same number of degrees* (fig. 3). When both eyes fix the central aperture the optic angle is 14° . A deviation therefore of the excluded eye to the extent of 5° , reduces the optic angle from 14° to 9° . From this it is easy to calculate that, while *accommodation* still remains in both eyes for a distance of 10 inches, the visual axes intersect at a distance more than half as much again (15.7 in.), and which, if it in turn became the point of fixation, would need $1\frac{1}{2}$ dioptries less of accommodation to be in exercise ($2\frac{1}{2}$ D instead of 4 D).² I have tried a sufficient number of cases to assure myself that *outward* deviation of the excluded eye is the *rule* where refraction is apparently normal or only slightly hypermetropic, though here and there an exception is found. Of ten recorded cases the average deviation was $4\frac{1}{2}^\circ$, as shown in the following table, which also gives the angular interval between each border of the blind area and the visual axis *before deviation*—the difference between them gives angular dimensions of the blind spot.

TABLE I.

No.	Inner border of blind area.	Outer border of blind area.	Breadth of blind area.	DEVIATION.
1.	$12\frac{1}{2}^\circ$	$18\frac{1}{2}^\circ$	$5\frac{3}{4}^\circ$	0°
2.	$12\frac{1}{2}^\circ$	$18\frac{1}{2}^\circ$	6°	1° or $\frac{1}{2}^\circ$
3.	$12\frac{1}{2}^\circ$	19°	$6\frac{1}{2}^\circ$	$2\frac{1}{2}^\circ$
4.	11°	17°	6°	4°
5.	$12\frac{1}{2}^\circ$	$18\frac{1}{2}^\circ$	6°	$4\frac{1}{2}^\circ$
6.	$12\frac{1}{2}^\circ$	$18\frac{1}{2}^\circ$	6°	5°
7.	13°	19°	6°	$6\frac{1}{2}^\circ$
8.	13°	$18\frac{1}{2}^\circ$	$5\frac{1}{2}^\circ$	7°
9.	$11\frac{1}{2}^\circ$	17°	$5\frac{1}{2}^\circ$	7°
10.	$12\frac{1}{2}^\circ$	$18\frac{1}{2}^\circ$	6°	$7\frac{1}{2}^\circ$
Average,				$4\frac{1}{2}^\circ$

If this table is at all representative (and I expect it is fairly so), it shows that, while deviation occurs in nearly all, its amount varies greatly in different individuals; in No. 10 only $6\frac{1}{2}^\circ$ of convergence is left, as attached centrally to the accommodative effort—less than one half. A more extensive set of observations is much to be desired to arrive at a more reliable average, and to seek, if possible, to note some of the *causes* of these variations, but for taking records the "direct method," to be described presently, is far to be preferred.

¹ Euc., bk. i. prop. 32.

² See the footnote on page 479.

It has been considered by Donders, a fact at present unaccountable, that only a *small* proportion of hypermetropes should develop strabismus, and that the *same* refractive anomaly should lead to squint in some cases and not in others. No doubt an explanation is afforded by these great variations which exist in the amount of convergence *naturally* attached to the effort of accommodation. So long as every hypermetropic eye was supposed to deviate inwards when excluded there was no reason why *all* hypermetropes should not squint. The *minor* degrees of deviation which the camera detects come thus to have importance. The advantages of angular measurements over linear ones are obvious. The latter would vary with camerae of different sizes, and would not permit of direct comparison, whereas the former are invariable.

It is evident from the results obtained that the central connection between the efforts of convergence and accommodation is still considerable, though not complete. If there were *no* central connection the excluded eye would deviate outwards nearly 14° instead of only $4\frac{1}{2}^{\circ}$. If the connection were complete it would not deviate at all. In ordinary vision there is perfect concert between the two efforts, since the two visual axes meet exactly at whatever point is accommodated for. To bring this about a "supplementary" effort must be in exercise whenever central connection is insufficient. This effort is connected with the instinctive desire for single vision, of which the seat is yet unknown, so that we may say the relatively *complete* convergence of ordinary vision is maintained partly by central connection with accommodation and partly by this additional effort, which is *first* roused into activity by the sensible presence of double images, and then *maintained* in exercise by the fact, of which the nervous centre is every moment kept sensible, that were the effort abated the mental image would immediately resolve itself visually into two. To keep it from doing so the joint sensations from the retinæ must all the while be bearing between them the message of continually impending (yet as quickly averted) double vision, by threats of double images so slight and frequent that they produce the required effect without our being conscious of their existence. It is difficult to conceive the exquisite mechanism at work so assiduously when

we remember that, if double images are produced artificially or by disease, it is impossible for the mind to tell to which eye each image belongs—whether, therefore, the visual axes are crossed or not, and whether convergence needs to be increased or relaxed to bring the images together.

By Hering's theory, convergence is a single effort, exerted in equal amount in each eye.

It is also clear that impressions from both eyes are necessary to maintain the supplementary factor in convergence connected with the abhorrence of double images. When, therefore, the obstructive in the experiment is placed before the right eye, and vision is confined to the left only, this common effort ceases, and *both* internal recti receive correspondingly diminished impulses from the converging centre. Were this all that happened, *e.g.*, in my own case, each eye would deviate outwards $2\frac{1}{2}^{\circ}$ as represented by the dotted lines in fig. 2. As a matter of fact, however, the active one remains stationary, fixing the central aperture, while the uncontrolled one moves outwards 5° .

This can be proved by commencing the experiment with *both* lateral apertures in their respective blind areas, when it will be found that if the stop is pushed to the right, although the right lateral aperture comes into view, the left one remains hidden the whole time; if the stop be pushed to the left the left aperture appears while the right one continues hidden, showing clearly that in each case it is the seeing eye which continues stationary, and the excluded one which deviates. Another innervation, therefore, distinct from that of convergence, must come into play to keep both the eyes from deviating equally. This is found in that centre whose ordinary function it is to turn both eyes to the right, and which, therefore, presides over the internal

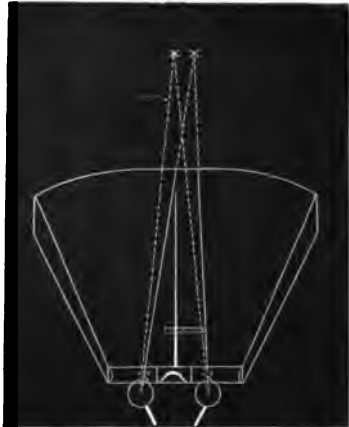


FIG. 3 A.—Convergence of the visual axis as if for the left hand cross is effected by the converging innervation; but they are jointly deflected to the right hand cross by the ranging innervation; in accordance with Hering's theory.

rectus of the left eye, and the external of the right eye. *It* compensates by a slight effort for those impulses which the left internal rectus has lost from the converging centre; but since it governs both eyes equally, while it maintains the convergence of the left eye, which would otherwise fall back $2\frac{1}{2}^{\circ}$, it moves the right eye through an additional $2\frac{1}{2}^{\circ}$ (see fig. 3 A).

The effort put forth by this fresh innervation is determined entirely by the requirements of the seeing eye; it only affects the deviating eye because it cannot help influencing one as much as the other. Its intervention is *proved* by the next two experiments. The result is that exactly half the deviation of the right eye is due to relaxation of the internal rectus, and the other half is due to contraction of the external rectus; but since in the left eye the *diminishing* converging effort and the *increasing* ranging effort have each to do with the internal rectus, it remains stationary.

EXP. 2.—With the stop in the *middle*, fix the central aperture with both eyes, and try to place the right forefinger exactly upon the central aperture from outside. The attempt will succeed in proportion to the perfectness of the observer's muscular sense. Now push the stop to the *right*, and repeat the attempt. The finger will be found to have missed its mark, and to be *actually* on the right side of it; and similarly to the left side of it if the stop is pushed to the left. The miscalculation will be *slight* if the attempt is made *directly* after the exclusion of the eye, and greater with every increase in the interval which elapses till the maximum miscalculation is reached, which in my case is about a distance which corresponds to $2\frac{1}{2}^{\circ}$ on the graduated scale. The right eye, we have seen, has meanwhile moved 5° . It may therefore be accredited as a rule that the angle of miscalculation is *half* that of the deviation of the excluded eye; it is slight at first, because the deviation is slight, and they increase together in the proportion of 1 to 2.

It has long been known that when one eye is closed, and a finger is pushed forward from under a book, it misses its mark to the side of the closed eye; but I believe this phenomenon will be absent in those with whom deviation of an excluded eye does not occur at the distance of the test; and that the extent of miscalculation will be found to depend entirely on the *amount* of the deviation, and to be half as great.

EXP. 3.—If the central aperture is very closely watched its apparent position may be observed to move slowly to the right as soon as the stop is pushed to the right. Now, it is remarkable that the point of view should *seem* to be moving when not only is the point really stationary but also the image it throws on the retina, and the retina itself. Since only one eye is in this case engaged in vision, and that

(as may be shown by the immobility of its blind area) keeps quite still the whole time, there cannot be the slightest change in the comparative *tension* of its recti, to account for the apparent movement of the image. Moreover, though the excluded eye deviates, we shall see later that the oculomotor muscular sense is purely *central* and not peripheral, since the *same* degree of tension in a muscle is mentally estimated or mentally ignored, according to the central source of the impulses which cause the tension. The stillness of the seeing eye therefore proves that the illusion is due to some alteration in central nerve effort of which the mind takes (what is now) unnecessary cognizance, and thus forms a false estimate.

The new effort is also shown by the nature of the apparent movement to be the one which the mind has been accustomed to associate with *lateral displacement* of the point of fixation, and with the *joint* movement of both eyes to the right, which such displacement makes necessary in the ordinary vision of nature. The illusion cannot be due to the diminution of converging effort, because *that*, as we shall see, is mentally associated only with the idea of *distance*, not at all with the angular departure of the object from the median plane, or its position in the field of vision. The *slowness* of the apparent movement is a striking feature; it shows how gradually the ranging effort is put forth, consistently with the gradual diminution of the converging effort for which it exactly compensates.

It is a fact which affords some food for thought, that although the *stimulus* which causes the "supplementary" converging effort ceases *suddenly* when the stop is pushed to the right, yet the *effort* itself continues for some time decreasing only *gradually*. This is in striking contrast to the speed with which full convergence is again effected when the stimulus is restored. The gradual relaxation of the converging effort when the stimulus is withdrawn, causes *both* internal recti to receive growingly feebler impulses from the converging centre, so that each eye has a constant and momentary tendency to deviate outwards, which is only prevented in the left one by the wonderful vigilance of the nervous mechanism which every instant appreciates this tendency, and as quickly compensates for it, *not* by again stimulating the flagging convergence, but by causing a strictly proportionate and gradual increase of that effort whose output causes in the mind the impression that the point of view (really stationary) is moving to the right. It need hardly be said that all this naturally accords with and establishes Hering's theories mentioned on p. 477. The apparent movement of the central aperture is *through half the angle and at half the rate* of the real movement of the deviating eye. A little reflection on the preceding experiment will show the truth of this, as nearly as it can be determined, and also that when an object is fixed not far from the middle line its position is mentally referred to the vertical plane which bisects the angle of convergence, and which, as we shall see, runs through a point midway between and slightly behind the centres of the two eyes. (See the line *yp* in fig. 3.)

After a few attempts to touch the point thus miscalculated, the

mind allows for the error, and the attempts begin to succeed. It has already been suggested that thousands of such attempts in childhood contribute to the wonderful correlation between the muscular sense of the eye and the hand. How perfectly they may by practice be made to co-operate is seen in a good cricketer or marksman.

The *senses* are there to begin with, but the mental apprehension of their import, both singly and jointly, seems to be largely left to be perfected by *education*. Indeed, it is known how any sense itself may be quickened by receiving a larger share of psychical attention, or dulled by its prolonged abstraction.

The human body is thus made capable of adapting itself within limits to adventitious circumstances; it is not made, like an ordinary loom, capable only when once set of turning out material of one texture,—but it is like a loom, if one can be conceived, made with such wonderful skill and forethought that it can automatically adapt itself to the requirement of any new material and other altered circumstances.

I find, on trying to touch the central aperture with my left hand, that when the stop is to the right, instead of missing its mark to the right side of the central aperture aimed at, it misses it to the left side, and when the stop is in the middle it misses it still more to the left side, though its miscalculation is not very precise. Its muscular sense is therefore less perfect.

EXP. 4. On first opening the eyes in the morning the divergence is greater than during the day; it falls just after the mid-day meal and perhaps after the others.

EXP. 5.—When vision is directed *through* either the central aperture or the left lateral one at an object placed at different distances, accommodation is, of course, diminished in proportion. It will be found that the excluded eye moves *outwards* with each *removal*, and *inwards* with each *approach* of the point of fixation. This shows how *delicate* is the connection between the two efforts, since the slightest difference in accommodation causes an alteration in the degree of convergence.

EXP. 6.—If convex glasses of increasing strength be placed in turn before the active eye, the blind area of the obstructed eye moves outwards with each increase in the refractive power of the lens employed. With *concave* glasses, on the other hand, it moves inwards with every increase. This experiment, of course, differs only from the last in the method employed; which, indeed, is far less satisfactory, owing to the fallacy introduced by prismatic action of the lenses, if their optical centres are not placed exactly in the line of vision—a precaution of great difficulty.

EXP. 7.—When the box is sloped downwards from the eyes, I have records which show that the deviation of the obstructed eye is reduced by 2° or 3°. I am not quite satisfied, however, with the observations—the bridge of the nose almost obliges the box to be held at a greater distance. The way to get over the difficulty would be to use prisms with their bases upwards, which would permit the

box to be held horizontally, and yet record the effect of a downward direction of the visual axes. The ordinary circular prisms used in practice are not available for this purpose, owing to the difficulty of placing the centre of the base exactly in the vertical line which bisects the prism. A slight shift to either side not only *reduces* the vertical deflection of the line of vision, but introduces a still greater *lateral deflection*, which vitiates the result. Small prisms fixed in the visual apertures would be most satisfactory.

EXP. 8.—If the central aperture be fixed by the left eye, with the obstructive to the right, it is possible to place the right lateral aperture so precisely upon the inner border of the right blind area that the point of light alternately appears and disappears, showing an evident tendency in the nerve centre to rhythmic, or at least irregular action. This irregularity furnishes a striking contrast to the fixedness of gaze and precision of movement in ordinary binocular vision. It devolves upon the supplementary effort in single binocular vision to fill in these irregularities in the fluctuating basis, besides meeting the new and changeful requirements constantly introduced in glancing from point to point. It is interesting to notice that this *fluctuating* effect in the converging centre is connected with the evolution of a *steady* stream of nervous energy from the accommodating centres. It may perhaps bear some comparison with the rhythmic automatism which manifests itself in the vasomotor centre under the uniform stimulation of venous blood, as evidenced by Traube's curves.

EXP. 9.—With both eyes fixing the central aperture, and with the obstructive in the middle, place the right lateral aperture in the outer part of the blind area at a definite number of degrees from its inner border. Push the obstructive to the right, and note how long a time elapses before the hidden point comes into view, by listening to a clock pendulum beating half-seconds. As might be expected from Exp. 8, the interval is a variable one. Thus, at one sitting, my right eye was engaged from $12\frac{1}{2}$ to 22 seconds in rotating outwards $3\frac{1}{2}^{\circ}$.

EXP. 10.—After wearing convex spectacles for some hours, I find that for a time the relative divergence is diminished (by the training the converging centre has undergone in the increased relative demand made upon its energies). How long this effect lasts I have not been able to observe.

EXP. 11.—*Measurement of the Blind Spot.*—I have found the angular dimensions of the blind spot in its horizontal meridian, as far as the box measures it, very uniform. In nearly all cases it was approximately 6° . So far as the observations are worth, they go therefore to confirm Landolt's estimate of 6° , rather than Helmholtz's of nearly 7° ($6^{\circ} 56'$).¹ The method they both employed was that of moving a pencil on a piece of paper till the point became lost to view. With one who has thoroughly practised indirect vision this suffices, but for others it is very uncertain. Thus Helmholtz says: "I have even seen men of education and information—doctors, e.g.—not able

¹ It must be remembered, however, that any error of the box from not measuring the exact horizontal meridian tends to give too *small* a result.

to prove the disappearance of small objects on the blind spot."¹ Hanover and Thomson, in 22 eyes (quoted by Helmholtz), found the breadth to vary from $3^{\circ} 39'$ to $9^{\circ} 47'$. I believe cases of less than 5° or more than 7° will be found exceedingly rare. In taking measurements, the stop should be either in the middle or to the opposite side of the eye under examination. I believe it is better to start with the point hidden, and let the observer exclaim at its first appearance at either border, rather than to note its disappearance, though the two may check each other.

A point of light is peculiarly fitted for the purpose, owing to the comparatively great susceptibility of the peripheral parts of the retina to light. Brewster² stated that astronomers, when they cannot see a minute star by looking *directly* at it, may often bring it into view by looking somewhat *away* from it. Landolt,³ however, finds "the perception of light remains almost exactly the same throughout the whole extent of the retina." He instances that in his right eye the perception of light at a part 30° from the centre remains the same, while the visual acuteness is reduced to $\frac{1}{16}$; but certainly, in my own eyes, the point of light appears to be more easily discerned on its emergence from the *inner* (macular) border of the blind area than from the outer border—it may not be so with others. *Clinically*, the measurement of the blind spot may be useful, both to determine the increase of the posterior staphyloma of progressive myopia and to trace the progress and decline of such affections as optic neuritis, in which the adjacent retina loses its perception awhile by infiltration.

A disadvantage is, that in the original instrument the two lateral apertures are not upon the same level, and therefore one of them (the highest) measures the blind spot *above* its horizontal diameter, and gives a uniformly smaller and fallacious record. This may be rectified by using, instead of slides, two flexible ribbons arranged circularly, so as to have the lateral apertures on the same level.

It is well to have the point coloured *blue*, since the peripheral parts of the retina perceive this colour most readily. If we assume that an angle of 4° , with its apex at the optical centre of a normal eye, subtends 1 mm. of the retina, then 6° would subtend $1\frac{1}{2}$ mm.; showing the close coincidence between the anatomical and physiological dimensions of the disc. The angular distance between the visual axis and the border of the blind area I have not found so uniform as the breadth of the blind spot. Landolt and Dobrowolsky found the interval greater in hypermetropes and smaller in myopes.⁴ It would be well to confirm this by the camera.

¹ *Optique Physiologique*, p. 735.

² Brewster on *Stereoscope*, 1856, p. 44.

³ Landolt, on *Examination of the Eyes* (translated by Dr Burnett, 1879, Philadelphia), p. 214.

⁴ *Examination of the Eyes*, Landolt, 1879, p. 216.

III. *The Direct Method.*

This method is far more useful clinically, and not less interesting physiologically. The eye is not placed in the dark, nor is the blind spot made use of. It depends upon the fact, that when each eye receives a single image upon its median vertical meridian, from whatever points they are thrown, the two are mentally referred to the same vertical line.

Exp. 12.—Place the *left* aperture out of sight and the obstructive to the right; the observer then sees the central and the *right* lateral apertures. As he looks, they appear to approach. The right slide is then pushed inwards till they seem to lie in the same vertical line. The process is now complete; it will be found that a *real* interval separates the *apparently* superimposed apertures. This interval expresses in degrees the relative divergence of the eyes, for one visual axis passes through one aperture, while the second lies either above or below the other. I have found this method quite easy in a child of six.¹



FIG. 3 E.—Illustrates the "direct method." The apertures *appear* superimposed though *really* separated by the deviating angle of the eye.

In comparing its results with those obtained by the blind spot method, I found that they coincided, showing that the mere additional presence of an image upon the retina does *not* affect the convergence and accommodation, so long as the desire to unite double images is eliminated. In the *blind spot* method there is an image in one eye, in the *macular* method in *both*. Its explanation is simple. Since the view of the right point by the left eye is intercepted by the median partition, and that of the central aperture by the right eye is cut off by the obstructive, each eye sees only one point, and that a different one, as shown in fig. 3 B. From the nature of the curve at the base of the camera, accommodation is required from each eye in equal amount (or practically so). If now the brain relationship were *complete*, when attention is directed to one aperture, say the central one, *both* visual axes would converge toward it, while the image of the right point would fall to the *inner* side of the macula of the *right* eye, and would be correctly referred *outwards* to its real position in space. This, in fact, does continue momentarily, when first the points are looked at. As soon, however, as relative divergence commences, and the right eye deviates outwards, the image of the right point approaches

¹ It is convenient for children to remove altogether the little wooden slides bearing the visual apertures.

the macula, or, more correctly, the macula approaches the image, for it is the eye which moves and not the point. While this is going on,



FIG. 4. —The direct method. Each luminous point throws an image on the fovea of the eye on the same side, so that both images are mentally referred to the plane which bisects the angle of convergence.

the two stationary apertures appear to be getting nearer to each other, for the cerebral centres are unconscious of the divergence, and make no allowance for it. The images do not appear to *meet* completely until each falls upon the median vertical meridian of its eye. It is well to begin the experiment with the apertures at some distance from each other, and after allowing a short time for them to approach naturally as far as they will, to push the right slide inwards, and let the observer say when they come into the same vertical line. In this part of the process the eye remains stationary while the image is moved, on to its median vertical meridian.

The dialogue would be

something like this :—

Q. What do you see?—A. Two bits of light.

Q. How far apart?—A. An inch or two.

Q. What happens? (pushing on the right slide slowly).—A. The right one is moving to the left.

Q. Say when they are *quite* together, that is, when the right point comes to be *exactly below* the left.—A. Now!

This concludes the observation. The *real* interval between the two points, automatically recorded by the graduated scale at the base of the box, has only to be read off to give in degrees the relative divergence of the eyes. This method dispenses with the use of prisms and the fallacies which attend them; it saves the trouble of special measurement, and gives an angular instead of a linear record, which is therefore always ready for comparison. It is equally available by daylight or artificial light.

But the best *practical* evidence of its efficiency is afforded by the ease with which it reveals the *physiological* prevalence of relative divergence in near vision, while the ordinary methods have only hitherto detected the grosser *pathological* exceptions. I may not be acquainted with all of them, and therefore cannot dilate the reasons of their failure, but I think I can suggest

what they are in Von Graefe's well-known test, which when carried out as usually directed, does not reveal the slightest relative divergence in my own eyes, though, as we have seen, 5° really exists on exclusion. I have not had access to Von Graefe's own directions. I may quote those in Mr Carter's valuable treatise on *Defects of Vision*, as I followed them:—

“In this more delicate test the object of vision is a small black dot, bisected by a vertical line. A card thus marked is fixed in the median line at a distance of 8 or 10 inches from the eyes, and the patient is directed to look at it steadily. A prism of ten or twelve degrees, with its base either upwards or downwards, is then placed before the eye; and as the power of the superior or inferior rectus to overcome double vision is very limited, this prism necessarily produces a vertical diplopia. The patient will therefore see two dots, one above the other. If the original convergence for the object is accurately maintained, the duplication of the vertical line will only cause it to appear elongated, and the two dots will be seen one above the other on the same line. If, on the contrary, the convergence be not maintained, the patient will see two lines with a dot upon each; and when the diplopia is a consequence of relative divergence of the optic axes, the double images will be crossed, and the extent of the divergence will determine the distance between them.”

On carrying out these instructions the dot truly duplicates and the line elongates, but that is all. The line still continues single. The reason of this becomes evident when the further step is taken of covering one eye for a short time; on again uncovering it, two lines appear, separated by a considerable interval, but they quickly run together again. This shows that the desire for fusion, though doubtless *weakened*, is not removed altogether, for the overlapping portions of the two linear images are sufficient to excite it. We shall see that images need not be similar in shape to excite an effort to unite them. Indeed, in ordinary vision the two pictures, as illustrated by the stereoscope, are slightly dissimilar except when the objects viewed are at a practically infinite distance. But I find if the upper part of the line be drawn very wavy, and the lower part straight, so that in the experiment the wavy portion overlaps the straight portion, there appears to be no attempt to unite them, though even then would not be quite sure that there is not a faint effort to keep them nearer to each other than they would otherwise be.

The fallacy may also be demonstrated in another way *without* temporary exclusion of either eye, by simply holding the line at

first horizontally (with the prism as before) and then quickly returning it to the vertical position; the two images for a moment or longer are quite separate, and hesitate a little before they run together.

"Why then," it may be asked, "if the test does not eliminate the fusion effort, does it *ever* reveal relative divergence?" It does so because, though it does not, like the camera, *remove* the desire for single vision, yet it lessens it to such an extent that it becomes inadequate to the demands made upon it in certain pathological conditions. The test *weakens* the desire for single vision, not only by the effect on one of the images of the slight light-absorbing (especially when the prism is not perfectly clean and free from moisture) and chromatic properties of the prism, but also by *shortening* the linear extent of the overlapping portions of the two images of the line. It would therefore detect relative divergence in such conditions as (1) those probably very rare cases in which the normal desire for fusion is defective. By lessening the desire still further it might be rendered incapable of rousing a sufficient "supplementary" converging effort. (2) Where the mechanical difficulties which attend convergence are so great that no effort can overcome them unless prompted by a *strong* fusion stimulus, as in some extreme cases of myopia, or where there is weakness of the internal recti or functional disability in their innervation. (3) Where almost the whole of the required convergence devolves on the fusion effort.

In all cases of myopia a larger share falls to the fusion effort than in the normal eye, because there is less demand for the effort of accommodation in looking at any point, and therefore the degree of convergence *due to central association* is correspondingly small. The smaller it is, the more work it leaves for the fusion effort, so that, "*cæteris paribus*," the greater the refractive anomaly the larger is the required proportion of supplementary or fusion effort.

A great effort needs a great stimulus. The latter is so weakened by the prism that, while still adequate for the requirements of normal refraction, it may be inadequate for those of high myopia, in which, moreover, mechanical difficulties almost always exist as well from the altered shape of the globe.

To make the test of any relative value even in these cases,

care must be taken to make the line of always the same length, or if not, to adjust its distance from the eyes in proportion; so that the reduplicated portion of the line may always be of the same length, and thus ensure *uniform* diminution of the desire for fusion, otherwise the test might at one time detect an insufficiency and at another time not. Moreover, the line which joins the apex and base of the prism must be exactly at right angles to the line uniting the centres of the two eyes (intercentral line); otherwise, though the lines continue parallel, their very opposition would only prove that convergence is *not* complete—if it were so, the lines would be *separated* by an interval determined by the strength and degree of rotation of the prism. Even when the *prism* is held correctly, if the *line* looked at is not also held exactly at right angles to the intercentral line another fallacy ensues, for the linear images, though still parallel are oblique, so that coincidence of their overlapping portions, instead of showing convergence to be complete, can only take place when it is incomplete, for were it complete an interval would separate them, varying as before with the degree of rotation of the card.

These difficulties, I would suggest, may be overcome by the use of a *double* prism composed of two prisms, each of 2° , fused together by their bases¹ (see fig. 5). The patient, shutting the left eye, holds this prism before the right one, and looks through it at a card marked with a single dot or *short* line. Two false images appear, one 2° above and the other 2° below the real position of the dot, and both are seen by the right eye. It is easy for the patient to hold the prism so that the two images appear in the same vertical line, and then when the left eye is opened as well to say whether the *real* image of the dot lies to the right or left of this line. Even if the first two are not held vertically, if all three images are in one straight line it shows that convergence is complete. If the central one lies to the right of the line, uniting the other two, there is relative *divergence*; if to the left, there is relative *convergence*.

Simple as this expedient is, and though it yields the same result as the camera, it is inferior to the use of the latter by the

¹ In reality, of course, it is a *single* prism of 176° though double in its use, since three faces are used instead of two. The large face (or base) should be towards the eye, the two smaller faces towards the object.

direct method. The camera ensures uniformity in the distance of the object from the eyes without the trouble of measurement ; it needs less intelligence in the patient, and gives an automatic angular record. The double prism, however, would I think be found useful for rough analysis at greater distances. The



FIG. 5.—Side view of the right eye and the double prism. The false images seen by the right eye are dotted. The central one is seen by the left eye.

radical difference between Von Graefe's test and the camera is that in the latter a *separate object* is used for each eye, while in the former the *same* object is reduplicated by a prism. The camera also not only reduces the desire for single vision, but abolishes it altogether when the lower of the two lateral apertures

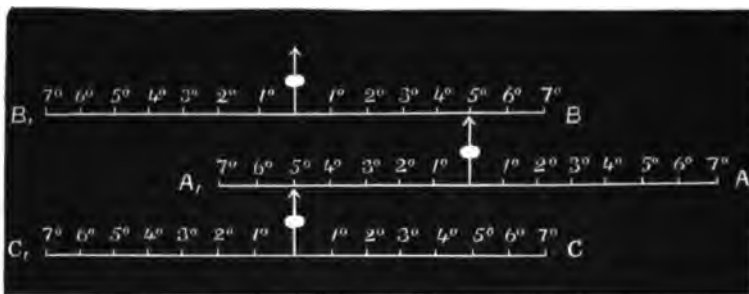


FIG. 6.—To illustrate how relative divergence is measured by the double prism. A is the only device on the card, and is seen by the left eye ; B and C are false images of it, and are seen by the right eye. In this instance 5° of deviation are seen recorded. If the two lowest arrows are made continuous by rotating the prism, the middle one points to *twice* the divergence, for as C moved to the right, B moves equally to the left, A of course remaining stationary. The arrows would all but touch the lines above them when the card is held at the appropriate distance of 10 inches.

is used in conjunction with the central one, so that the eye takes a position determined solely by the converging effort which is associated with the accommodation.

If when, in the "direct method," the two images are in the same vertical line, as in fig. 3 B, an effort be made from outside to place the finger on them, it will miss both, for it will be just half-way between the two actual apertures, which, though they *appear* superimposed, are, as we have seen, really separated by an interval of nearly an inch, so that the vertical plane in which the two images appear to lie is that which bisects the angle of convergence, as represented in fig. 4. At present we have only to do with movements of the eye in the horizontal plane, and with the head stationary. The converging apparatus appears to be solely connected with the union of double images and the estimation of distance. With the relative position of points along the horizontal meridian of the field of vision it has nothing to do. This must be determined entirely by—

(1) The part of the retina on which images fall.

(2) The innervation which turns both eyes to the right or left.

As regards the *first* indication, since each image falls on the median vertical meridian of its eye, the effect is the same as though they were both thrown from one vertical line, for which convergence were complete; and, since the relaxation of the converging effort is not taken into account, there is no reason why the images should *not* be referred to the *median plane*, for there is nothing so far to give any preponderance in favour of either side.

As regards the *second* indication, however, as seen in fig. 3, while convergence occurs to the left-hand cross, both axes are directed to the right-hand cross by the ranging innervation of which the mind *does take cognisance*. Now, the inclination of the plane which bisects the angle of convergence, to the median plane, exactly represents the angular effect of the ranging energy which is in exercise—hence the images are referred to this line. It is now easy to observe the fluctuations in the stream of nervous energy noticed with the blind spot method on p. 487, for one point continues to make tiny excursions to the right and left of the other, though without any regular rhythm. This makes it useless to take very exact records in minutes and seconds. It is also clear that a more accurate method is scarcely to be desired, since it would only magnify

these irregularities. Care must be taken that the difference in level of the two apertures is enough to avoid continued effort to unite them. It is remarkable that, when their vertical separation is only *slightly more* than enough to prevent optical union, *a tendency may be noticed for them to keep near the same vertical line*. Even when one is pushed a little way to the right or left the other is apt to follow it, and this in spite of their dissimilar *shape*. It is even noticeable when the apertures are *coloured* differently; but disappears very rapidly with increasing vertical separation of the two points, and is not in my own eyes detected in the slightest degree when the *lowest* of the two lateral apertures is the one employed, in conjunction with the central one, which is, of course, the highest of the three, being separated from the *lowest* movable point by an angle of $2\frac{1}{4}^{\circ}$ (from the eyes), and from the *highest* point by slightly less than 1° , in the camera with which I experimented. This latter interval is one which can be overcome at times by the superior or inferior rectus in order to satisfy the desire for fusion, especially when the eye has succeeded a few times, and acquired the facility. After allowing it to do this for a time, the following experiment may be made:—

EXP. 13.—Place the stop to the *left*. Let the left aperture be as before entirely occluded, and the right one be placed 3° or 4° away from the central aperture. Look through the camera thus for about a minute, during which interval the *right* eye sees *both* the images, and the *left* *neither*, so that the latter is deviating outwards.

Now, push the stop from the left to the right. This proceeding *transfers* the view of the central aperture from the right eye to the left one, which, being deviated 5° , miscalculates its position, and refers it to the *right* of the other point still seen by the right eye. The two points thus separated now by a small interval run together, though to do so it is clear the relative divergence is diminished by a slight converging effort. If to start with the right lateral point is placed 6° away from the central one instead of 4° when the experiment is repeated, though the points appear separated by the same interval as before yet their position is of course reversed; yet they still run together. In this case the relative divergence is *increased* to meet the desire for fusion, instead of being diminished. Whether this is brought about by inhibition of the centres for the internal recti, or by antagonism of the external, remains yet to be found out.

EXP. 14.—Were the right lateral aperture, to start with, placed 5° away from the centre, and the last experiment repeated with the stop to the left, the two points would appear separated by nearly an

inch, and with the stop to the right they would appear in the same vertical line. This enables the observation of a patient by the "direct method" to be easily confirmed, for all that is needed after taking the observation to ensure that fusion effort is eliminated, is to push the stop back to the right, and again to the left, to see whether the point at its first reappearance occupies the same position as before.

EXP. 15.—Use the *highest* lateral aperture on the right side, and with the stop to the right, move it till it meets and appears to fuse with the image of the central aperture. After fusion, push the right brass slide inwards slowly and steadily, and it will be found that the two blended images move to the left together, for the one which really moves carries the other with it to preserve fusion, and this goes on until the moving aperture travels right up to the central one, or at least as near to it as the construction of the box will permit, so that even this *false fusion* has sufficient power to undo the whole of the relative divergence.

If on the other hand the brass slide with the movable point it bears is drawn *outwards*, resolution of the two images does not occur till the points themselves are *really* separated by 10° . The desire to continue the false fusion is thus strong enough to *double* the previous divergence. Albeit the experiment makes the eyes water and feel uncomfortable. Whether this discomfort is due to *peripheral* antagonism of two sets of muscles, the external recti and the internal, I cannot tell; or whether it is due to a *central* struggle to overcome by inhibition a nervous connection probably never before invaded to that extent. Perhaps if the two points were on the same level the attainable divergence might be still greater. As it is, the deviation of 10° brings the eyes to within 4° of parallelism. This false fusion is of the same nature as that described by Sir D. Brewster, when, in looking at a patterned wall it is possible to converge the eyes for a point so far behind, or in front of the wall, that fusion of the laterally adjacent patterns takes place. The strength of the effort put forth to *maintain* accomplished fusion is much greater than that instigated by the desire to unite the two images when they are separated to begin with. The relative divergence attainable by the present experiment is much greater than, and must not be confused with, that attainable by the effort to overcome a prism, for in the latter case the two images are separated to begin with by the act of placing the prism before the eye. It may be deduced from what has preceded that, when the brass slide bearing the right luminous point is drawn outwards or pushed inwards, the *fused* images appear to follow at *half the rate*. But if they are *not* fused only one of them appears to move, and that at a rate *equal* to that at which the slide travels; the difference being that in the latter case both eyes are stationary, whereas in the former, while the left eye remains fixed the right one moves at the same rate as does the brass slide which bears the point of light it perceives. If the slide is moved jerkily slight momentary separations of the images result. If the effort to maintain false fusion be so strong, probably that to maintain *true* fusion is greater still. To measure it a camera should be used with two apertures at the same level, or else with a prism let

into one of the small wooden slides before the eyes to just rectify the difference in level. It is the effort to maintain *existing* fusion which is tested by the common practice of approaching a finger to the eyes till one of them rolls out, though in this test *accommodation* increases at the same time, while in the camera accommodation is unchanged. I may note in passing that in my own eyes the nearest point of *single* vision by the finger test is closer to them than that of *distinct* vision, which illustrates a fact almost self-evident, that the relative divergence which occurs on the exclusion of one eye does not indicate deficiency in the converging function itself, but only in the *link* which connects it with accommodation. Accommodation assists convergence, and convergence accommodation, but they do so *only* through the central link which connects the two efforts, and enables one to influence the other. The slighter the link the less the effect one has on the other—but that has nothing to do with the individual strength of either.

Donders has shown that hypermetropes fix more easily when they look through prisms which make them converge more strongly. Is this because the converging effort assists that of accommodation by means of the central link between them? Apart from any pathological affection of either centre it is reasonable to suppose, since the sympathy is mutual, that if accommodation exerts only a weak influence on convergence, convergence will have a correspondingly weak influence on accommodation; a unit of either will contribute less than usual to the other.

If this be so, relative divergence, as revealed by the camera, since it indicates imperfection in the channel of mutual assistance, would lessen the advantage of the prisms above mentioned—though it would remove in their use all fear of their causing squint. But this is theory and needs practical confirmation.

A little confusion has arisen from the incorrect supposition that the *strength* of the *internal recti* is tested by prisms base outwards, and the ability to overcome them; whereas it is the conditions of the converging reflex as a whole which are thus estimated, including the existing intensity and activity of the desire for single vision. This is clear from the fact that when both eyes are directed to the right or left the contraction of the internal rectus may be greater than can possibly be attained by converging effort, the innervation called into play being a different one. Inability to overcome such prisms of high power *might* of course be due only to weakness of muscles, but in that case the ranging and converging movements would be equally impaired. Moreover, since accommodation remains unchanged, such prisms only indicate the limits of attainable relative divergence or convergence, which depend largely on the strength of the central nervous connection between convergence and accommodation. Approaching the finger to the eyes till one rolls outward is another method of testing the strength of converging effort, though *still* it is not the efficiency of the internal recti only that is indicated, but of the whole converging sensory-motor apparatus—afferent, central efferent, muscular, and mechanical. Strength of fusion effort is also influenced

by the nature and doubtless by the size and number of the images to be fused, as well as by the amount of attention directed to them.

Exp. 16.—There are some cases of strabismus, especially of the divergent kind, in which, as Donders has pointed out, the mind becomes conscious of the direction of *each* eye. Such a person can correctly calculate the position of any object seen by either eye, and, indeed, employs one or the other just as convenience requires, being able to distinguish very readily which he is using for observation.

In testing a case of slight external strabismus with the camera, one would rightly expect to find that when the two images by the direct method are in the same vertical line there would be a very great interval between the actual apertures. This would be so in recent cases, or any in which one eye is disused in ordinary vision, for however much deviation might really exist, the images on both maculae would still be mentally referred to the same vertical line.

But in cases like those mentioned by Donders the fact is that the eyes *correctly* estimate the distance between the two apertures, so that the images do not appear superimposed at all, unless the apertures themselves are made so, which the construction of the camera does not quite admit. The axis of the deviated eye does not follow the moving point of light, but correctly estimates its position as its image travels along the retina. An instance of this rather puzzling anomaly was tested with a camera by Dr Joseph Bolton. The "direct method" is useless for such cases, and will not detect even any deviation, being like the usual prismatic ones too subjective; but the "blind spot method" enables the exact position of either eye to be noted. A careful examination of a few of these cases might yield interesting results. All that is necessary to discover them is to try the two methods and see whether their records differ.

Exp. 17.—When the two images in the "direct method" are looked at for some time with a dim illumination they may be observed to alternately disappear altogether. This favours the current view that the part played in vision by the visual apparatus of the two eyes alternates in intensity; as each in turn becomes tired, the other gives it a rest.

Exp. 18.—While looking at the two images by the "direct method" shut the right eye; the image seen by it moves upwards and to the left, showing the eye itself has moved downwards and to the right. Why?

Exp. 19.—To ascertain the *rate* of the deviation of an excluded eye. With the stop to the right, and the right luminous point a considerable distance from the centre, look through the camera till convinced that no more deviation will occur. Move the right point inwards till its image seems just below the other, and *leave it in position*. After a timed interval of rest, take up the camera again and look at the central aperture with the stop *in the middle*, listening to the beats of a clock pendulum. At one end of a beat push the stop to the right, and count the number of seconds which elapse until the two luminous points meet, for the right one has been left in position all the

while. The interval varies considerably in different cases and at different times, from half a minute to a minute and a half. In one case the total divergence of $6\frac{1}{4}^{\circ}$ appeared to take from 68 to 73 seconds.

In the same case, when the two points were separated to begin with by 5° , the images took 40 seconds to meet. When separated by 2° they took 5 to 8 seconds. In this way the rate can be estimated for each degree. It is clear that the eye deviates outwards with *diminishing rapidity*, at any rate in the latter parts of the deviation.

IV. Central Method.

EXP. 20.—Place *both* lateral apertures out of sight, and use the central one only, looking at it with the stop to the *right*, for some seconds. Then push the stop quickly to the left. The first image disappears, and a second one takes its place to the left, at a distance from the former determined by the degree of divergence which has occurred. *Each* eye rotates through the same angle, sometimes as quickly as the stop is pushed, sometimes not until after an appreciable interval.

This is proved by repeating the experiment with the right luminous point out of view to start with in the right blind area, while the stop is to the right. This hidden test-point sometimes springs into view when the stop is pushed to the left almost simultaneously with the appearance of the left image of the central aperture, but sometimes not till a moment or two after. With the stop to the *right*, the *left* eye fixed the central aperture while the *right* deviated. Pushing the stop to the *left* excludes the *left* eye and lets the *right* eye see, so that either at that moment or a little later both eyes swing through an angle equal to the deviation, to let the right eye fix and the left eye deviate. Why, then, does the new image of the central aperture not seem to move? Because the *converging* innervation is unaffected by the change, and to it alone are all false estimates in the camera primarily due. The only innervation called into play for the movement in question is the "ranging" one, of whose efforts the centres are so well-informed that though the eyes move the image does not seem to. So wonderfully is the correction made that even in nystagmus, though the eyes continually oscillate unknown to the patient, he never, according to Helmholtz, sees fixed objects moving. So truly, also, through the higher centres does the mind estimate the amount of this effort which is in exercise, that artists are said to be able to judge more correctly the lateral distance between the two objects by glancing rapidly from one to the other, than by any other visual method.

EXP. 21.—To ascertain *how soon* the deviation begins. Let a thin strip of india-rubber connect one end of the stop with the left side of the box, while a piece of string passes from the other end of the stop round the forefinger of the right hand. Give the string, to begin with, just such a degree of tension as to keep the stop in the *middle* while both eyes look through the camera at the central aperture. Listen

to a clock pendulum beating half-seconds. At one end of a beat pull the stop instantaneously to the right, and at the other end of the beat let it fly back to the left; in so doing it exposes a transitory double image of the central aperture, or at least a perceptible widening. This shows that divergence has commenced *in less than half a second*. In how *much* less still remains to be noted, which may be done by shortening the pendulum; but great quickness of observation would be needed to attain any degree of accuracy.

EXP. 22.—Let the central aperture be alone used, and push the stop, alternately from left to right and right to left, at definite intervals. If the intervals are not too short relative divergence sets in, as shown by the apparent displacement of the image to right or left at every movement of the stop. The vision of the central aperture is alternately monocular and binocular, the proportion between the two being determined by the *rapidity* of each movement and the *length of the interval* between them. At certain rates the relative divergence gradually *increases*, as shown by the greater and greater apparent displacement with each excursion, which proves that a certain proportion of binocular vision to monocular is required to overcome the natural tendency to divergence. The desire for single vision is, as it were, *diluted* by interruptions. There appears to be a certain rate at which the relative divergence neither increases nor diminishes, and a quicker one still at which, if divergence is present to begin with, it slowly diminishes, and yet a further rate at which it does not appear at all; but a mechanical apparatus would have to be used to obtain really reliable results. The width of the stop, of course, greatly affects the proportion of binocular vision, as also does the length of its slit. If the stop were just wide enough to cut off in the *middle* of its course the view of the central aperture by both eyes, vision would be wholly monocular; with each diminution of size there would be a larger proportion of binocular vision.

It may be that this method would furnish a comparative means of estimating the efficiency of the fusion centre, by noting the *amount* and *nature* of the dilution required to make the desire for fusion incapable of preventing either the occurrence of relative divergence or its continuous increase. Two points would have to be considered—the *frequency* of the interruptions, and the *length* of each; the former would depend on the *number* of side to side movements per minute, the latter on the *rate* and *length* of each movement, the *pause* at the end of each, and the *width* of the stop. It is possible that a certain *duration* of the two pictures in the brain is necessary to elicit the desire to fuse them at all.

If a wide stop were used, and an up and down movement given to it in the slit, binocular vision would be diluted, not by monocular, but by intervals of no vision at all. Whether the result would be the same I do not know.

EXP. 23.—If, after looking at the central aperture for a little time with the stop to the *right*, the latter then be pushed quickly to the middle, the central aperture appears duplicated for a moment by the

addition of another image to the left, and the two run quickly and with equal velocity into one. The appearance of this second image shows, of course, that the eye has deviated. The apparent angular separation of the two images is equal to the angle of deviation. If they could be kept in their first position (and this we shall see may be done), an effort to touch the right one would place the finger $2\frac{1}{2}^{\circ}$ to the right of the middle line, and an effort to touch the left would show it to be likewise $2\frac{1}{2}^{\circ}$ to the left of the middle line. We have seen how when the stop was at first pushed to the right, and the right eye deviated 5° , that the only then existing image of the central aperture seen by the left eye appeared to move till it was referred $2\frac{1}{2}^{\circ}$ to the right of the middle line. The right eye was then *excluded*, but now, when the stop is put back in the middle, it receives an image on the retina 5° to the right of the macula, and which is therefore referred 5° to the *left* of the image seen by the left eye.¹ Since the latter image appears $2\frac{1}{2}^{\circ}$ to the *right* of the middle line, the former must be $2\frac{1}{2}^{\circ}$ to the left of it. The left eye remains stationary throughout, while the right one (no longer excluded) now returns through the same angle through which it deviated. Why, then, if the right eye *only* is moving, and that through an angle of 5° (and this is it easy to verify by testing the positions of the *blind* areas), does *each* aperture appear to traverse an equal angle of $2\frac{1}{2}^{\circ}$? It is just the *undoing* of what happened when the obstructive was pushed to the right. Then the image seen by the left eye seemed to move *slowly* to the right for $2\frac{1}{2}^{\circ}$; now it *quickly* appears to return, because the desire for single vision has aroused the supplementary converging effort, which so affects the innervation of the left internal rectus that there is no longer any need for that effort which usually turns both eyes to the right; it therefore ceases, and just as the mind took cognisance of its introduction, and imagined the point seen to move to the right, so it takes cognisance of its cessation, and refers the point again to its original position. In like manner the second image (seen to the left by the right eye) though it traverses 5° of the retina, only *seems* to move $2\frac{1}{2}^{\circ}$, because that is the only moiety of the movement which is due to cessation of the mentally-recognised ranging effort; the other half being due to positive converging effort, of which no mental account is taken as regards horizontal position. Half the movement of the deviated and returning eye is due to relaxation of the external rectus, and the other half to increased contraction of the internal rectus. The former is taken into account mentally, the latter is not. It is quite clear from this that the oculo-motor muscular sense is *purely* central, for the *same* contraction of a muscle is appreciated or not according to the *central* source of the effort.

EXP. 24.—(a) Place the right lateral aperture, to begin with, 4° or 5° away from the central one, and the stop to the left. Two images are now seen by the right eye, the right lateral and the central one, and their *relative* distance is correctly estimated, though the position of both is miscalculated $2\frac{1}{2}^{\circ}$ to the left. Now push the stop in the *middle*; this uncovers the deviated left eye, and reveals another image of the central aperture miscalculated $2\frac{1}{2}^{\circ}$ to the *right*, so that it appears

¹ These angles have their apex at the principal dioptric centre.

just above the right lateral aperture, which is miscalculated $2\frac{1}{2}^{\circ}$ to the left, as we saw. But the two images of the central aperture are only thus separated for a moment, for they quickly run together, and normal fusion takes place.

(b) If, however, instead of starting with the stop to the *left*, the stop be first placed to the *right*, and then replaced in the middle, the images do *not* run together, though the relative position of the three points is exactly the same as before. In the latter trial, the desire for false fusion at the near distance is greater than the desire for true fusion at the greater one; but why it should not be so in the first trial I cannot certainly explain. It may be that the desire for false fusion of two objects not in the same vertical line takes longer to develop its strength than that for true fusion, and has not time in the first trial to do so before the movement for the fusion has begun. The effect of attention, as seen in Exp. 26, has probably more to do with it. From the construction of the camera, the vision of the right lateral aperture cannot be other than monocular, so there must be only one image of it, but the vision of the central aperture, though *monocular* when the stop is either to the left or the right, is *binocular* when it is replaced in the middle, so that, deviation having in the meanwhile occurred, there are two images of it. The only difference between the two trials lies in the *order* in which these two images appear. In a third modification they may be made to appear simultaneously.

(c) Push inwards the left brass slide till it just occludes the central aperture. Let the right luminous point (now the only one visible) be placed as before, and the stop in the middle. On quickly drawing out the left brass slide both images of the central aperture appear at once, and generally run together, though the result depends somewhat on the position of the right lateral point and the amount of deviation that has been permitted to occur. This experiment may be repeated with many variations by anyone desirous of ascertaining the laws of fusion; the left lateral aperture, *e.g.*, may be used instead of the right, and each in different positions, or both may be used.

Exp. 25. To ascertain the effect of *attention* on the desire for single vision. Place the right lateral aperture, coloured blue, $2\frac{1}{2}^{\circ}$ to the right of the central one, which is covered with a piece of paper or ground glass, and therefore white. On looking into the camera with the stop in the middle, the two points are seen in their true positions, the white one appearing nearly half an inch to the left of the blue one. Now push the stop to the right; the two images begin to move slowly together till they come to be in the same vertical line, and again separate by each pursuing its movement till they have just changed places. The white image is now nearly half an inch to the *right* of the blue one. When the stop is replaced in the *middle*, another white image appears nearly half an inch to the *left* of the blue one, which now has a white image on each side of it, and at equal distances from it. If, while moving the stop, *attention* is directed to either of the *white* images, they quickly run together, while the blue returns to its original position. But if the attention is concentrated on the *blue* point the whole

time, the white ones do *not* run together, but remain as at first, one on each side of the blue one. This shows that the mere *presence* of double images, when they are perfectly well defined, does not excite the desire for single vision, unless one of them becomes the special object of attention.

If the blue point is not exactly halfway between the two white ones, move the brass slide which bears it until it becomes so, and then read off its angular position, which, when doubled, will give the angular deviation, or relative divergence of the eyes.

This, then, is the *third* method of measuring it by the camera, not of any clinical value, but useful as showing that the deviation is practically the same in extent under such varying tests, for—

(1) In the “blind-spot” method there is one image upon the fovea of *one* eye.

(2) In the “direct” method there are two images, one upon the fovea of *each* eye.

(3) In this “central” method one eye receives an image on its fovea, and each eye receives an image away from its fovea.

It would be wearisome to recount more experiments, as the use of the camera permits of so many variations. Before passing to the next section on “Distant Vision” it may be well to give a convenient summary of the results obtained in near vision.

1. When one eye is excluded from vision and placed subjectively in the dark, it nearly always deviates outwards (Exp. 1).

2. The same deviation occurs if *each* eye is made to receive an image or any number of images, provided that the desire for fusion is in abeyance (Exp. 12).

3. The average angle of deviation appears at present to be about $4\frac{1}{2}^{\circ}$ with vision for 10 inches.

4. There are four methods of measuring this angle—three by the camera, and one by a double prism modification of Von Graefe’s test.

5. When the record by the “blind-spot” method differs from that of the other three, it is because the mind has learnt to estimate the position of each eye separately (Exp. 16).

6. There are reasons why Von Graefe’s clinical method has not revealed *physiological* divergence.

7. The divergence begins in less than half a second (Exp. 21), and continues gradually at decreasing speed (which may be measured at any point) for from half a minute to a minute and a half (Exp. 19).

8. Half the deviation of the excluded eye is due to contrac-

tion of its external rectus, the other half to relaxation of the internus.

9. The oculo-motor muscular sense is purely central; the same contraction of a muscle is mentally appreciated in one way or another according entirely to the central source of the effort (Exp. 23).

10. The truth of Hering's theory that the horizontal movements of the eyes are governed by two innervations, each acting on both eyes as a single organ, is repeatedly demonstrated.

11. The object fixed by the seeing eye appears during the deviation to move in the same direction; the apparent movement is at half the rate and through half the angle of the real movement of the excluded eye (Exp. 3).

12. An image on the fovea, whatever the real position of the eye, is referred to the plane which bisects the angle of convergence, and which therefore passes through a point midway between and slightly behind the centres of the two eyes (Exp. 2 and 3).

13. A fixed object seen by a stationary eye may appear to move, and the same fixed object seen by a moving eye may appear stationary according to the innervations in play.

14. The degree of deviation which occurs on exclusion is greater in the early morning, often falls after meals, and is subject to oscillations, according to conditions which affect the nervous system.

15. A large degree of convergence is still centrally connected with the accommodating effort, though its amount differs greatly in different persons, being in some more than twice as much as in others.

16. It is probable that these differences account for the fact that squint develops in many cases of hypermetropia where there is less refractive abnormality than in other cases where squint shows no tendency to occur.

17. The connection between the converging and accommodating efforts is still very delicate; the slightest alteration in the latter is accompanied by an alteration in the former (Exp. 5).

18. The degree of convergence centrally attached to accommodation is subject to slight waverings (Exp. 8). It may to a certain extent be either increased or diminished by the desire to

unite two images, and to a still greater extent by the desire to maintain their fusion (Exp. 13 and 15).

19. Images at slightly different levels in the two eyes, even when the difference in level is great enough to prevent their fusion, are often kept near each other by the desire for it.

20. This tendency decreases rapidly with increasing difference in level, and is not perceptible with the images separated by a vertical angle of 2° or 3° .

21. The desire for this false fusion at a near distance may be greater than the desire for true fusion at a greater distance, though this is affected by the *order* in which the desires are roused (Exp. 24).

22. When the images are *coloured* differently the desire for fusion is weakened but not altogether removed.

23. The desire for single vision can be interrupted to any required extent by causing alternations of binocular and monocular vision, so regulated that, with different rates, deviation may be either prevented, retarded, arrested at any part of its course, or made slowly to retrogress (Exp. 22).

24. The effect of *attention* exerts a well-marked influence on the desire for fusion (Exp. 25).

25. The ordinary test of placing a prism (base in or out) before one eye estimates simply the degree of relative divergence or convergence which is attainable by the desire to rectify the diplopia created by the prism, and which is compatible with the existing effort of accommodation.

26. Approaching a finger to the eyes tests the power of *maintaining* existing fusion with proportionately increasing accommodation. This is true up to the nearest point of distinct vision, within *that* it tests the relative convergence attainable by the desire to maintain fusion complicated with increasing indistinctness of the images.

(To be continued.)¹

¹ The writer will be greatly obliged for the pointing out of any omissions and errors detected in this paper.—Address, E. E. Maddox, M.B., *Shipton, Chipping Norton, Oxon.*

A CONTRIBUTION TO SPLENIC HISTOLOGY. By
ROBERT ROBERTSON, M.D. (Edin.), *Assistant Physician to
the Ventnor Consumption Hospital.* (PLATE XV.)

(THE following observations were made in 1879 while working under Dr D. J. Hamilton in the Pathological Laboratory of Edinburgh University. Circumstances have prevented a resumption of the work hitherto, hence the incomplete form of the present paper.)

Controversy in splenic histology of late has mainly centred about the minute structure of the splenic pulp, and the manner in which the circulation is carried on therein. It cannot yet be said that the channels by which blood reaches the veins from the arteries have been determined beyond dispute. W. Müller¹ is the representative of those who maintain that the capillary plexus, which in other organs intervenes between arteries and veins, is in the spleen replaced by an adenoid reticulum through which the blood filters in its passage to the veins, the arteries ending by their endothelial lining becoming continuous with the cells of the reticulum, while in the veins the fibres of the reticulum gradually approximate until the vessel wall and its endothelial lining are again complete. Others again, while agreeing with this view as to the absence of a continuous system of vessels, differ in details,—Billroth,² for instance, holding that the arteries terminate by open mouths in the reticulum of the tissue which intervenes between the "capillary veins;" Klein,³ more recently, denying the presence of a reticulum of fibres, which he says is an appearance due to section of the septa of a honeycomb of membranes.

On the other hand, Kölliker⁴ and Grohe⁵ maintain that the

¹ Stricker's "Human and Comparative Histology," *New Syd. Soc.*, 1870, vol. i. p. 357.

² "Zur normalen und pathologischen Anatomie der Menschlichen Milz," *Virch. Arch.*, vol. xx. p. 413.

³ "Observations on the Structure of the Spleen," *Quart. Jour. Micr. Sci.*, vol. xv. p. 368.

⁴ *Manual of Histology*, p. 369, London, 1860; *New Syd. Soc.*, p. 451.

⁵ "Zur Geschichte der Melanémie nebst Bemerkungen über den normalen Bau der Milz und Lymphdrüsen," *Virch. Arch.*, 1861, vol. xx. p. 325 *et seq.*

circulation in the spleen is carried on in a precisely similar manner to that of all other organs of the body; that is to say, there is a continuous system of vessels out of which, except by rupture, the blood never passes; that the arteries break up into capillaries, which are again continuous with the minute veins. But while Kölliker thinks it probable that an endothelial lining, too delicate to be demonstrable in the finest vessels, is continuous throughout, Grohe thinks that a layer of fusiform cells is the only lining membrane.

The uncertainty which these opposing views excites is increased by the difficulty of explaining completely by either certain appearances found in the pathological condition known as "diffuse waxy spleen." Stained with methylaniline iodine, a section of such a spleen shows, even under a low power of the microscope, that the organ consists in great part of an infinite number of canals and their intervening septa. Sections of these canals, in all directions, transverse, longitudinal, and oblique, are recognisable, bounded by limiting lines of rose-stained "waxy" material, and if the disease is in an early stage between two adjacent rosy lines, a blue portion of the septum forming a narrow strip of apparently retiform tissue can easily be found. Are these canals with their intervening septa adventitious appearances due to the morbid condition, and if not, to what do they correspond in the normal organ?

To determine this question, the spleen of a healthy young adult was examined. The organ was markedly "congested," but in no other respect peculiar. Hardened in dilute chromic acid and stained with logwood, sections were half cleared up in clove oil, and then mounted in dammar. By this method the canals or vessels were demonstrated which had already been seen mapped out by morbid material in "waxy disease," but without "half-clearing" in clove oil the canals could not be recognised. In the septa and walls of these canals cells were seen, which, when isolated, had large rounded or more or less ovoid nuclei, surrounded by a small quantity of matrix substance, and projecting on the inner border of the narrow band or fibre into which the matrix substance was prolonged on either side of the nucleus. The general outline of the inner border, except where the nucleus bulged, was concave; the opposite border was con-

vex and wavy, refracting the light; the ends of the fibre were occasionally found curled towards the inner border, not unlike what is seen in fibres of yellow elastic tissue. In the section these cells were seen arranged side by side in the long axis of one of the "canals" referred to, so as to form an apparently continuous membrane, and transverse section may thus show a row of "leucocytes" projecting towards the lumen of the canal.

In the septa the coloured blood-corpuscles, often in linear arrangement, and nucleated cells and fibres gave the appearance of an areolar tissue (such, indeed, Billroth regarded it, though he ultimately abandoned the view that the capillaries end in it by open mouths, finding that they pierced the canal walls.

There exists then in the splenic pulp an abundant canal system, the canals being of considerable size, and separated by septa usually relatively small and of loose fibro-cellular structure. The walls of these canals consisting largely, so far as we have yet seen, of peculiar fusiform cells with nuclear body projecting towards the inner aspect of the cell.

To ascertain the relation of this canal system to the arteries, various methods of injection from the artery were tried with spleens of pigs and sheep. It was found very easy with fluid injection to drive the liquid freely out through the vein, but on preparation of sections of these spleens, the tissue was seen to be very unequally permeated by the injection fluid; and in those parts where the injection had entered most freely the appearance was that of a general infiltration of the tissue with the injection; no arterial branches except those of larger size could be made out.

On injecting, however, by the vein with an open cannula in the artery it was discovered that after sixteen ounces of the liquid had been thrown into the spleen of a sheep not a drop came out through the artery. The cannula in the vein was then closed, and further injection attempted from the artery, but only a very small quantity could be forced in, though in the attempt the cannula was driven off the syringe. Additional injection through the vein was then tried, and with ease another 8 oz. of fluid was thrown into the organ before the capsule ruptured.

Double injection was also tried, blue gelatine mass being

thrown into the veins, and when this was cold a carmine injection mass into the arteries. The special object in view was to inject the capillary plexus of the Malpighian bodies from the artery; and on naked eye examination of a section of the injected organ it seemed probable that this had been accomplished successfully, for the Malpighian bodies were conspicuous by their carmine colour in an area of dark blue. On microscopic examination, however, no injection of the Malpighian capillaries could anywhere be found, but everywhere a zone of carmine surrounding the uncoloured Malpighian body, and separating it from the dark blue of the injected pulp-substance.

Injection with carmine mass of a human spleen in an early stage of waxy disease was tried also. The injection was thrown into the artery only, and after hardening, sections were stained with methylaniline, and mounted. It was hoped that, the canals being mapped out by the morbid material, the relation of the injected arterioles to them might be more easily discovered. This hope was to a certain extent realised on examination of sections microscopically. It was found that minute injected vessels ran in the septa between the canals, and such a vessel was seen after running for some considerable distance in the middle of a septum bifurcating, and the two branches diverging approached the walls of canals, and one partly encircling a canal in transverse section was lost sight of just when apparently about to pierce the canal wall.

Injection of sheep's spleens with $\frac{1}{2}$ per cent. nitrate of silver solution was also tried, and in this connection it may be mentioned that in injecting from the artery a zone of pigmentation was obtained around the Malpighian bodies, corresponding to the carmine zone in the double injections described above.

Thus we have seen that the splenic arteries do break up into minute or capillary vessels which run for a considerable distance in the septa that intervene between the canals already described, and sooner or later they approach closely to the walls of these canals; and probably pierce them. In the Malpighian bodies it would seem that the surrounding pressure empties the capillaries of their contents, the injection appearing in the portions of the canal system with which the

Malpighian body is related, and with which its vessels apparently communicate.

We have also seen that some valvular arrangement exists, which, while it permits the blood or injection fluid to flow freely from artery to vein, prevents a return current from vein to artery. What this arrangement probably is we shall presently see; in the meantime it is necessary to consider the endothelial lining of the arterial capillaries and of the canal system.

A fresh sheep's spleen was injected from the artery with $\frac{1}{2}$ per cent. solution of nitrate of silver, and portions of the silvered tissue afterwards carefully teased out. In such specimens the endothelial lining of the arterial capillary was well demonstrated, and in a few specimens it could be traced until an infundibular expansion of the vessel took place to twice or three times its previous size. Nuclear bodies lying in the long axis of the capillary vessel outside the endothelium were found to belong to fusiform cells like those already described in the walls of the canals, and where a capillary vessel had been broken across, the curled end of one of these cells might be found projecting beyond the endothelium. The difficulty of demonstrating the continuity of the endothelium of the arterial capillaries with that of the canal system was due to the excessive delicacy of the walls of the canals, which, during the preparation by teasing, generally became entirely broken up, and to the elasticity of the spleen in lower animals, which prevented the ready demonstration of the canal system in sections of silvered spleens. Fortunately the spleen of a healthy human adult was obtained and injected five hours after death, and silvering of the endothelium by injection of the artery with nitrate of silver solution was successfully accomplished.

The tissue was hardened in dilute chromic acid and in spirit, and preparations half cleared up in clove oil, and mounted in dammar, were examined. The tissue was also examined by teasing in the fresh state after exposure to light. It was found that the arterial capillaries were lined by an endothelium, as already described in the sheep's spleen, but that unlike their infundibular expansion in the sheep's spleen, the vessel ended in an abrupt expansion (or flange), producing an appearance like the end of a candlestick.

On examination of hardened sections, stained with logwood, and mounted as described, the canals were found to be lined with an exceedingly delicate endothelial layer of cells, the outlines of the cells being faintly silvered, their shape long and narrow, and arranged generally across the direction of the canal, while outside this endothelium the fusiform cells, with their nuclei stained blue, were arranged in the long axis of the vessel.

Under a power of 1000 diameters, circular openings of small vessels could be seen with a clearly maintained continuity of endothelium. In some places the opening of the small vessels into the canals was conical to some extent, but this did not appear to be commonly the case.

Having thus traced the continuity of artery and venous canal, and shown that a continuous and unbroken endothelial lining does exist, we can now understand by what arrangement regurgitation from veins to arteries is prevented. It has been mentioned that the septa in which the arterial capillaries run are relatively small as compared with the size of the canals, and that they present a loose fibro-cellular texture. By distending the venous canals with blood or other fluid, these septa are pressed upon, the lumen of the capillary vessels becomes obliterated, and the liquid can neither flow back through them, nor can any pass from the arterial side, except by the use of very high pressure. The relative size of the two sets of vessels sufficiently explains how when no more fluid could be driven into the arterial system in the experiment described, a third more than the organ then contained was easily injected by the vein, and the organ ruptured.

Malpighian Corpuscles.—These bodies have been incidentally referred to, as mapped out by an injected zone, in silvered human and sheep's spleens, and in double injection of the spleen. This injected zone was in all cases sharply defined towards the Malpighian body in the condensed stroma of the pulp, but passed gradually away into the surrounding pulp-substance.

In the injected spleen of a cat the plexus of capillaries in the Malpighian body was well seen, and it was observed that they formed loops towards the periphery, from which branches passed

into the pulp-substance beyond. This zone of injection, therefore, is no doubt the fluid which has passed into the Malpighian capillaries, and, by surrounding compression, has been forced into the canal system of the pulp, with which the capillaries communicate.

In "half-cleared" sections, stained in logwood, the continuity of the stroma of the Malpighian body with the tissue of the septa of the pulp-substance was recognised.

So that the Malpighian bodies are, as it were, localised overgrowths of the tissues of the septa which separate the venous canals, cells and fibres multiplying, and the arterial capillaries, instead of bifurcating, breaking up into a plexus; but the stroma and capillaries maintain their continuity with the adjacent septa and canals, only, from compression by the overgrowth, these latter are condensed and form what was thought formerly to be the capsule of the Malpighian bodies.

EXPLANATION OF PLATE XV.

Fig. 1.—Endothelium of funnel-shaped junction of arterial capillary (*a*) and venous canal (*b*), from sheep's spleen (silvered). ($\times 450$.)

Fig. 2.—Spleen of woman injected with nitrate of silver five hours after death, showing expansion of arterial capillary (*a*) into a venous canal (*b*); the outlining of the endothelial plates is well seen. ($\times 450$.)

Fig. 3.—Small portion of tissue from same spleen, $\times 800$; *a*, venous canal, with silvered marking of endothelium; *b*, arterial capillary; *c*, section of vessel in communication with both *a* and *b*.

Fig. 4.—Arterial termination (waxy spleen $\times 450$); *a*, mouth of minute arteriole; (*b'*, *b''*, *b'''*), venous canals; *c*, nuclei of fibre cells; *e*, waxy infiltration of wall of canal.

SUPERNUMERARY LEG IN A MALE FROG (*Rana palustris*). By FREDERICK TUCKERMAN, M.D., Amherst, Massachusetts. (PLATE XVI.)

I FIRST wish to thank Professor Warner of the Massachusetts Agricultural College, to whom the frog belongs, for his kindness in placing it at my disposal.

The remarkable abnormality about to be described occurred in a frog which was blown, while blasting with gunpowder, out of a crevice in a ledge of mica schist 12 feet below the surface. It was immediately picked up, and, apart from being stunned, had apparently sustained no injury.

The same explosion also brought to the surface five other frogs, of different ages and sizes, none of which were killed or injured.

At the time of its unexpected appearance the frog was supposed to be about a month old. From this time until it was killed, two months later, it was not observed to eat anything.

The external opening of the crevice in the ledge measured only a few lines at its widest point, and flowing into it was a small stream of water, which undoubtedly conveyed either the eggs or the frogs in the larval stage to the interior of the rock, as the breach in the ledge was much too small even to admit the passage of a very young frog.

The pigmentation of the skin covering the extra limb corresponded in form and colour with that of the rest of the body, with the exception that the dark brown bands or spots towards the distal end of the leg completely encircled it. It was attached to the trunk slightly to the left of the mesial line, and to the left of the posterior end of the tip of the urostyle, just above the opening of the cloaca. The first part, about a line in length, seemed to be chiefly tegumentary in character, and was quite narrow. This was followed by an enlargement $2\frac{1}{2}$ lines in length, and a little less in width, chiefly in a ventral direction. Then came a second constriction greater than the first, which immediately widened into a large oval-shaped dilatation or sac, $\frac{3}{4}$ of an inch in length and $\frac{3}{8}$ of an inch in width, the walls of which were

not at all tense, and offered less resistance to pressure than was the case in the first enlargement. The space within was partially filled with fluid. It was quite evident, however, that it contained something else beside fluid, for, when rested upon one end, it not only kept its oval form perfectly, but could not be possibly depressed in the direction of its long axis. The remainder of the limb to the distal tarsals was straight, and measured $\frac{1}{2}$ an inch in length and $\frac{1}{3}$ of an inch in width. It was jointed above and below. The superior articulation admitted of but slight movement, the inferior was quite movable. There were two digits present, the inner one the longer, and a rudiment of a third. The usual position of the toes was that of adduction.

The limb measured, from the point of its attachment to the trunk to the tip of the last phalanx of the inner digit, $2\frac{1}{4}$ inches.

The circulation of the blood in the web between the two digits, as seen with the aid of the microscope, presented nothing unusual in appearance.

When stimulation was applied to the distal end of the limb, or to any part of it, the frog would usually draw itself, or jump quickly away, dragging the extra limb after it. Sometimes, however, often-repeated stimulation would call forth a slight muscular contraction in the limb itself, and this was occasionally seen to take place when the animal was left entirely to itself. The distal end of the limb would then be abducted a little to the right, the toes would partially separate, and at the same time a slight drawing of the whole limb toward the trunk would be perceptible.

The following appearances were observed on opening the limb:—

The narrow portion close to the point of attachment to the trunk contained a few tendons, blood-vessels, and a nerve. The tendons took their origin from the symphysis pubis. The blood-vessels could not be made out with any degree of certainty, with the single exception of a vein which appeared to join the left pelvic vein. The nerve was apparently a division or branch of the sciatic. In tracing it down the limb no division of it above the knee could be discovered, nor were any lateral branches made out. The space in the first enlargement was almost

completely filled by a mass of muscle to which the tendons belonged, and in which the vessels ramified. Neither bone (*femur*) nor cartilage were present at this point. The second constricted portion, smaller and narrower than the first, contained the tendons, vessels, and nerve, which it conveyed to the parts beyond. Within the large oval-shaped sac was a bundle of muscles running the entire length of it. There were no adhesions uniting the skin to the subjacent parts except at the ends. Two-thirds of the space not occupied by muscles was filled with a yellowish-red fluid, having a slightly acid reaction, and quite rich in red and colourless blood-corpuscles. The muscles were somewhat smaller than usual, and a few were wanting; but otherwise they presented no special variations from those found in this region. The gastrocnemius, tibialis posticus, peroneus, and tibialis anticus were easily distinguished. On cutting away the muscles a bone (*crus*) was brought into view. The shaft was long, cylindrical, and very slender. No groove was detected indicating the line of union between the fibula and tibia. The articular expansion at the inferior extremity was very large and out of proportion to the shaft above it. This formed a movable joint with the articular process of the bone below it. At the superior end of the shaft was an articular process, quite small, which had only a tendinous connection with the region above it. In the proximal tarsal region the skin adhered quite firmly to the parts below it. The muscles were much atrophied, and the vessels and nerves could not be clearly followed. In place of the usual two elongated bones (*astragalus* and *calcaneum*), connected above and below by epiphyses, there was a single long bone, unmarked by any longitudinal groove, articulating slightly with the ankylosed (?) tibia and fibula.

At the distal end of the bone no extra ossicles were found. The right digit was composed of a metatarsal bone and two phalanges. The inner digit (would be the fourth counting from the *hallux*), the longer, consisted of a metatarsal bone and three phalanges. The rudiment corresponded to the middle digit.

From this description it will be seen that the foot belonged to the right side of the body, although the limb sprang from the left side.

With the exception of the accessory limb the frog appeared to be in a perfectly normal condition.

EXPLANATION OF PLATE XVI.

It was found necessary, in order to show the rudimentary digit well, to turn the pes over, thus bringing the dorsal surface into view.

1. Enlargement filled with muscles corresponding to the position of the femur.
 2. Sac partly filled with fluid containing muscles and crus.
 3. Proximal tarsal region composed of a single long bone.
 4. Rudiment of the middle digit.
-

[*Editorial Note.*—The malformation in this very remarkable frog will, without doubt, recall to some of our readers the case of Jean Battista dos Santos, a native of Portugal, who visited this country in 1865, being then in his nineteenth year, and whose case was described in the *Lancet* of July 29, and subsequently by the late Dr P. D. Handyside, in the *Edinburgh Medical Journal*, March 1866. In Dos Santos's case of imperfect double monstrosity there were two complete sets of external organs of generation in addition to the intermediate lower limb. A case of a somewhat similar kind, in a female foetus, but with two lower limbs, was described by Von Baer, in *Mem. de l'Acad. de St. Petersb.* VI. Series, and his figures are reproduced in Förster's *Missbildungen des Menschen*, Jena, 1865. The writer of this note had also the opportunity of seeing, in February 1885, through the courtesy of Mr R. Urquhart, Lecturer on Pharmacy, Edinburgh, a new-born child with a similar deformity. The child lived a few days, but no dissection of it was permitted by the parents.—*W. T.*]

THE NATURE OF THE RELATIONSHIP BETWEEN
UREA FORMATION AND BILE SECRETION. By
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the University of Edinburgh.*¹

(From the Physiological Laboratory of the University of Edinburgh.)

IN a previous paper, published in the last numbers of this *Journal*, vol. xx pp. 114 and 267, I endeavoured to demonstrate that a direct relationship existed between urea formation and bile secretion. It is now necessary to inquire into the manner in which these two processes are thus connected. In investigating this subject we must remember that the bile constituents and urea are produced in the liver, and that our attention therefore must be directed to changes occurring in this gland.

The chief functions of the liver are the formation of glycogen and the secretion of bile, and the latter of these functions may be divided into two elements, the production of bile acids and the elimination of the effete blood-pigment as bilirubin. I shall endeavour to show that urea formation is connected with the latter of these, the excretion of effete hæmoglobin.

That blood-pigment is converted into bilirubin and excreted by the liver as such is clearly demonstrated by the work of Frerichs, of Städeler, of Kühne, of M. Herman, and others.

Tarchanoff was perhaps the first (*Pflüger's Arch.*, Bd. ix. pp. 53 and 187) to connect this production of bilirubin with an increased flow of bile. After injecting 100 c.c. of a dilute solution of hæmoglobin into the veins of a dog with a biliary fistula, he observed an immediate and enormous rise in the amount of bile and in the quantity of bile pigments excreted. A similar rise was observed after the injection of distilled water, which set free hæmoglobin by dissolving the blood-corpuscles. He observes that, while the bile pigments were so greatly increased, the bile acids were diminished in amount.

Stadelmann (*Arch. f. Exp. Pathol.*, Bd. xv. p. 337) records a

¹ Towards the expenses of this research, a grant was made by the British Medical Association on the recommendation of the Scientific Grant Committee of the Association.

similar series of experiments in which he injected hæmoglobin in much larger quantities, and in much more concentrated solution—20 to 40 grammes in a 20 per cent. solution. He observed that the bile first became thick and viscid, and that its rate of excretion diminished, the percentage amount of bile pigments being enormously increased. This initial fall was followed in a few hours by a great increase. Obviously the results of these experiments are to be explained by the large quantity of hæmoglobin used, and the concentration of the solution in which it was injected. By the increase in the solid constituents of the bile its passage along the bile ducts was markedly impeded, and it was only upon a more fluid bile being produced that it escaped freely and allowed the increased secretion to manifest itself.

In Tarchanoff's experiments, on the other hand, the hæmoglobin reached the liver in a dilute solution and in moderate amount, so that no blocking of the bile passages by the viscid bile occurred.

Such methods of injecting hæmoglobin in solution are by no means satisfactory, since the altered condition of the specific gravity of the blood and the changes in the circulation possibly induced, tends to vitiate the results obtained.

Employing the method of injecting into the blood some powerful hæmolytic, such as toluylendiamin, Afanassiew (*Ztsch. f. Clin. Med.*, Bd. vi. H. 4) has shown that the bile secretion is greatly increased. And in a paper, published in *Pflüger's Archiv.*, Bd. xxx., he says:—"Da nach Ergebnissen der Versuche mit Toluylendiamin die Gallenbildung durch massenhaften Zerfall der rothen Blutkörperchen gesteigert wird—tritt den Gedanken nahe, dass, unter normalen Verhältnissen, der Zerfall rothen Blutkörperchen, selbstverständlich innerhalb bestimmten physiologischen Grenzen, ein Anregung zur Gallen-secretion gebe."

Paschkis (*Wiener Med. Jahrb.*, 1884, S. 293) has further shown that these well-known blood-corpuscle-destroying agents, the salts of the bile acids, are exceeding powerful chologogues.

All evidence on the subject, therefore, goes to show that the destruction of blood-corpuscles, and the consequent setting free of hæmoglobin in the blood, does lead to a great increase in the secretion of bile.

That urea formation also is connected with destruction of

blood-corpuscles was first suggested by Führer and H. Ludwig (*Vierordts. Arch.*, Bd. xiv. S. 307) while Addison in 1864 (*Brit. Med. Jour.*, vol. i. p. 202), reasoning from different data, came to the same conclusion. The arguments of these authors are full of fallacies, and the facts upon which their theory is founded are capable of various different interpretation.

More recently Meissner, in a paper entitled "Ein Beiträge zur kenntniss des Stoffwechsels im thierischen organismus (*Ztsch. f. rat. Med.*, Bd. xxxi. S. 234), adduces very strong evidence for the production of a great part of the urea in the liver from blood-pigment. It is impossible to discuss fully this long and ably reasoned paper, but one or two of his arguments must be mentioned here.

No tissue of the body functionates so long as the blood,—to the last moment of life. The urea excretion during starvation also keeps up in like proportion. Now, fresh corpuscles must be constantly manufactured up to the last moment of life, and when food no longer supplies the material the muscles and fat are then used. That during the period of inanition blood-corpuscles are being destroyed is shown by the fact (Bidder and Schmidt) that a not inconsiderable amount of bile is formed up to the time of death, and it is no longer doubtful that the biliary colouring matter are derived from the hæmoglobin. On the other hand, the blood-corpuscles do not diminish much during starvation. Since Voit found that in a cat the blood lost only 4·8 grms. of fixed substances, a much smaller loss than is sustained by any other tissue in the body. Panum also found a relatively small reduction of the quantity of blood, and no diminution in the corpuscles during starvation. The lymph stream also persist till death, and in the lymph system blood-corpuscles are formed. The chief argument for his theory of the formation of urea he considers to be its appearance in the liver, and the relation of the formation and destruction of blood-corpuscles to the liver—the former very doubtful—the latter certain, the liver being the only organ of the body where a copious destruction of the blood-corpuscles can be detected. The fact which before all other supports this destruction in the liver, is the separation of bile pigments which are derived from the hæmoglobin (see Funke's *Lehrbuch der Physiol.*, 4 Aufl. Bd. I. S. 262). David has shown that it is undoubted that destruction of blood-corpuscles

occurs in the liver (*Ein Beiträge zur Frage über die Gerinnung des Lebervenenblutes*, Dorpat, 1866). He entirely denies their formation in the liver.

Meissner's arguments are of no small value, because they are founded on well-established facts, such as the connection of the bile secretion with blood destruction on the one hand, and with urea excretion on the other; and on the formation in the liver of both bile and urea.

That hæmocytes really are broken down in the liver has been, since the appearance of David's paper, definitely shown by Nicolaides (*Arch. de Physiologie*, T. x. p. 531, 1882), who found a very marked diminution in the number of corpuscles in the portal vein, a diminution which, during active digestion, was frequently as great as from 1,000,000 to 2,000,000. In four observations made on *fasting animals* this difference was found to be much smaller.

In investigating this connection between urea formation and excretion of hæmoglobin as bilirubin by the liver two methods are open to us. We may either directly inject hæmoglobin and study its effect on the urea excretion, or we may destroy blood-corpuscles within the body of the animal by the administration of drugs which have outside the body been proved to have hæmolytic action.

In order to avoid the infliction of pain, I have adopted the latter method.

For the purpose of breaking down corpuscles I have employed pyrogallic acid, and the salts of the bile acids, the direct influence of which on hæmocytes has been for long well known.

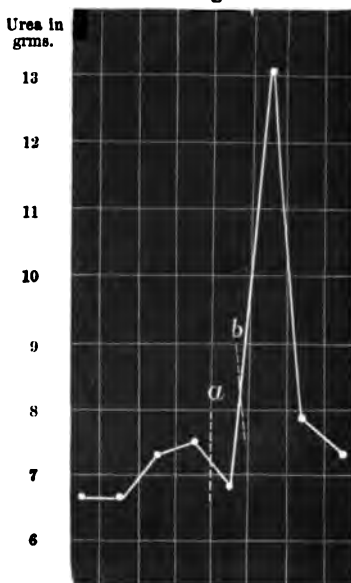
In these experiments healthy dogs in a state of nitrogenous balance (stickstoffgleichgewicht) were used, and a detailed account of the method of observation will be found in the *Journal of Anat. and Physiol.*, vol. xx. p. 268.

Exp. I.

A healthy setter bitch, weighing 14·96 kilos., had been kept upon a diet of porridge and milk till the urea excretion became constant. Pyrogallic acid was then administered by the mouth. Its influence on the urea excretion is shown in the accompanying chart and in fig. 1.

Day of Exp.	Quantity of Urine in c.ca.	Sp. G.	Urea in grms.	Remarks.
1	{ 765 - 6·734	1011	7·404	Weight of dog = 14·96 kilos. Diet—Oatmeal, 113 grms. Milk, . 320 c.cs.
2		1010	6·064	
3	885	1009	7·363	1 grm. pyrogalic acid. 1·5 grm. " "
4	855	1009	7·463	
5	810	1009	6·966	
6	975	1012	13·182	
7	780	1009	7·956	
8	{ 835	1009	7·480	
9	{ 835	1009	7·480	

Fig. 1



Exp. I.—Influence of pyrogalic acid on excretion of urea.
1 grm. given at *a*, and 1·5 grm. at *b*.

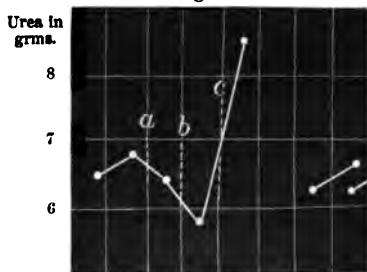
Exp. II.

In the second experiment I employed the mixed salts of the bile acids—the ordinary “crystalline bile” derived from ox bile. This was given by the mouth, and hence only acted when exhibited in large doses, since, as we know, much of these acids is decomposed in the intestines, and therefore a small part is absorbed unchanged, and in a form capable of destroying corpuscles.

The same dog was used, and the conditions of the experiment are precisely similar to those in Exp. I.

Day.	Urine in c.cs.	Sp. G.	Urea in grms.	Remarks.
1	650	1019	6.500	Weight of dog = 14.96 kilos.
2	750	1009	6.600	Diet as in previous Exp.
3	660	1009	6.468	2 grms. crystalline bile.
4	580	1010	5.742	2.5 " " "
5	600	1014	8.640	6 " " "
6	380	1015	—	
	considerable quantity lost			
7	860	1008	6.656	
8	690	1011	7.404	
9	840	1010	6.064	

Fig. 2.



Exp. II.—Influence of salts of bile acid on urea excretion.
2 grm. given at *a*, 2.5 grm. at *b*, and 6 grm. at *c*.

These experiments show that the action of these hæmocytic agents is accompanied by an increased production of urea.

But more than this is required to establish the fact that this increase is solely and purely due to the destruction of blood-corpuscles. We must be able to show a definite relationship between the number of corpuscles destroyed, *i.e.*, the amount of hæmoglobin to be excreted, and the urea produced. I have accordingly undertaken the following experiments, in which the urea was daily estimated and the hæmocytes daily enumerated before and after the administration of some hæmocytic agent, in order that a calculation might be made of the increase in the production of urea on the one hand, and the amount of hæmoglobin liberated on the other.

From such a method of research only approximate results can be expected, since, in the first place, the only available method of enumerating the hæmocyte, by Hayem's or Gower's hæmocytometer, is not absolutely correct. In addition to this, for such a

research as the present, where the object is to ascertain the total number of corpuscles destroyed, the disturbing element increased production, which in all probability follows increased destruction of corpuscles, just as it follows any loss of blood must tend to vitiate results. During the first day or two of any increased destruction, this increased production will make itself less felt than after the economy has had time to attempt to re-establish the normal condition.

Another source of fallacy, which must be borne in mind, is the difficulty of calculating the amount of hæmoglobin in relationship to the weight of the dog. In estimating the amount of blood, I have followed Bischoff and Welcker, and in regard to percentage of hæmoglobin present I have accepted Preyer's results (*Die Blutkrystalle*).

Two hypothetical formulæ have been suggested to represent the disintegration of the hæmoglobin molecule. That of Zuelzer (*Untersuch. ü. die Semilogie des Harns*, Berlin, 1884) need not here be considered, since it implies a great production of bile acids, which, according to the observations of Tarchanoff and of Stadelman, does not occur. Charles (*Brit. Med. Jour.*, 1885, vol. i. p. 820) suggests the following decomposition of two molecules of hæmoglobin:—

	C ₁₂₀₀	H ₁₉₂₀	N ₃₀₈	Fe ₂	S ₆	O ₃₅₈	+ 501 O	+ 182H ₂ O	+ 6H ₂ SO ₄	- Fe ₂ O ₃	
							C.	H.	N.	O.	
2 Bilirubin,	64	72	8	12	
150 Urea,	150	600	300	150	
32 Glycogen,	960	1600	—	800	
26 Carbonic Acid,	26	—	—	52	
							1200	2272	308	1014	

It is interesting to observe that in both these hypothetical decompositions a process of oxidation is supposed to occur, a fact which fully agrees with Ehrlich's recent experiments in regard to the reduction of methyl blue in the liver as well as in the lungs (*Cbt. f. Med. Wissensch.*, Feb. 21, 1885).

C,	.	54.00		Fe,	.	0.42
H,	.	7.25		S,	.	0.63
N,	.	16.25		O,	.	21.45

Considering the percentage composition of hæmoglobin from these data we may calculate the initial amount of hæmoglobin in the blood of an animal, and the amount set free by the disinte-

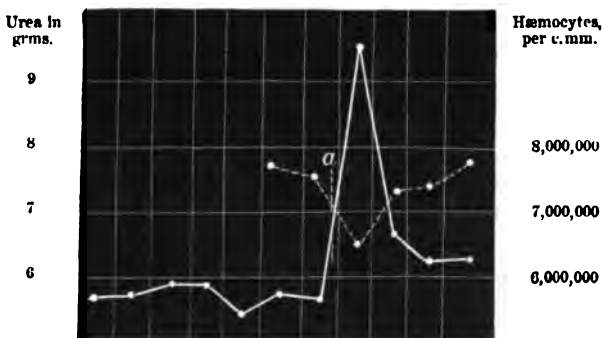
gration of corpuscles, we see that 200 grms. of this substance corresponds to 32.5 grms. of nitrogen, and from the above formulæ it appears that about 4 grms. must go to the formation of bilirubin, leaving 28 grms. to supply the nitrogen of urea. So 200 grms. of hæmoglobin may thus yield 60 grms. of urea,—the percentage of nitrogen in urea being 46.6,—that is, 1 gm. of urea will represent 3.3 grms. of hæmoglobin.

Exp. III.—PYROGALLIC ACID.

In this experiment a large black retriever, weighing 15.43 kilos, was used. The diet and details of the experiment are given in the accompanying table and figure:—

Day of Exp.	Urine in c. cs.	Urea in grms.	Hæmocytes per c. mm. of blood.	Weight in kilos.	Remarks.
1	500	5.800			<i>Diet.</i> —Oatmeal, 169.8 grms. as porridge. Milk, 320 c. cs.
2	500	5.800			
3	565	5.998			
4	565	5.998			
5	400	5.450			
6	455	5.643		15.42	{ 2 grms. of pyrogallie acid urine dark in colour— no albumen. Urine still dark.
7	455	5.643	7,460,000		
8	600	9.483	6,615,000		
9	485	6.617	7,275,000		
10	475	6.220			
11	475	6.220	7,270,000	15.42	

Fig. 3.



Exp. III.—Influence of pyrogallie acid on urea excretion and the number of hæmocytes. 2 grms. administered at a.

Before the administration of the drug the corpuscles were 7,460,000 per c. mm., but at the end of the second day, after the exhibition of

pyrogallie acid, they fell to 6,615,000. Now, the blood of a dog is about $\frac{1}{13}$ of its weight, therefore in this case the dog had 1186.3 grms. of blood. The hæmoglobin, according to Preyer, is in the dog 13.8 per cent. of the weight of the blood—in this case probably a little less, as the corpuscles did not reach the usual number, about 7,800,000 to 8,000,000, which would make the percentage about 13.4 instead of 13.8, and the weight of the hæmoglobin 129 grms.

Now, under the administration of the drug the corpuscles fell from 7,460,000 to 6,615,000, so 15 grms. of hæmoglobin must be set free; and since 3.3 grms. of hæmoglobin equal 1 grm. of urea, this will equal 4.54 grms. of urea, an amount corresponding very closely to the actual increase of 4.556 grms. for the two days.

Exp. IV.—PYROGALLIC ACID.

For seven days before the exhibition of the drug the dog, a healthy setter bitch, had passed on an average 7.679 grms. of urea per diem. The corpuscles at the end of the 6th and 7th day were 7,866,000, and 7,850,000, being an average of 7,860,000 per c.mm. The weight of the dog was 13.607 kilos. Calculating from Bischoff's results we see that the blood weighed 1046 grms., which will, according to Preyer, contain 144.348—say 144 grms. of hæmoglobin.

On the 8th day 2 grms. of pyrogallie acid were given, and another 1.5 grm. were administered on the 9th day.

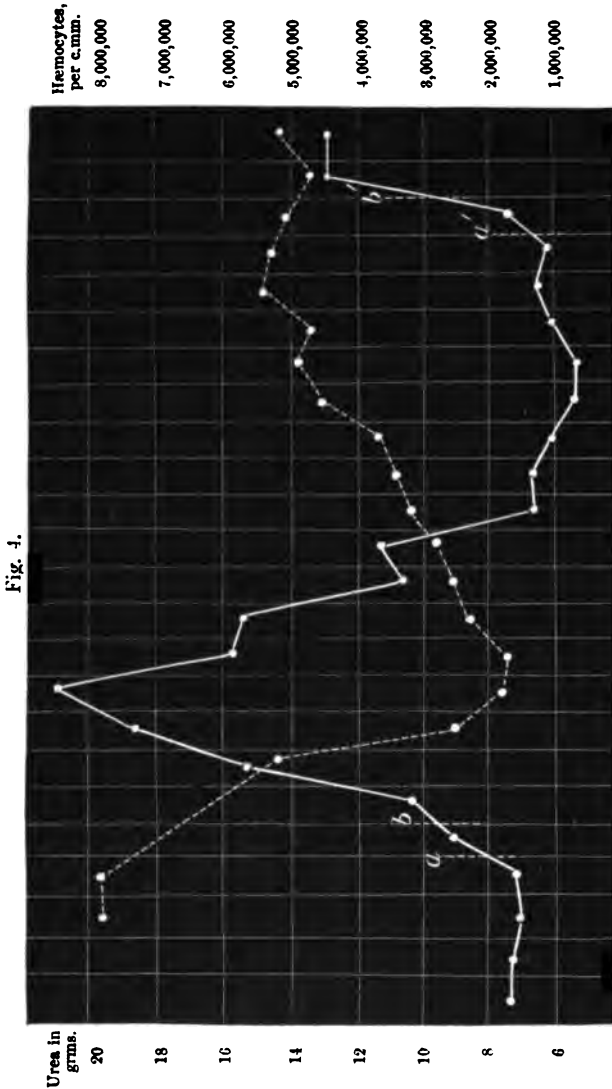
At the end of the 10th day the corpuscles had fallen to 5,190,000 per c.mm., indicating a destruction of 2,670,000 per c.mm. Calculating from the above data we find that this indicates a liberating of 48.9 grms. of hæmoglobin. And as we have already seen that 3.3 grms. of hæmoglobin is equivalent to 1 grm. of urea, we should expect to find, if all the hæmoglobin was excreted as bilirubin urea, &c., an increase of 14.6 grms. of urea above the normal. But a considerable part of the hæmoglobin escaped the action of the liver, and was excreted in the urine as such. Accordingly we find a rise of only 11.855 grms. of urea above the normal.

During the next twenty-four hours the corpuscles fell to 2,604,000 per c.mm., indicating a further liberation of 40 grms. of hæmoglobin, corresponding to 12.1 grms. of urea. But the urine still contained blood-pigment and we find an increase of only 10.855 grms. of urea.

Next day the corpuscles fell from 2,604,000 to 1,876,000, which represents the liberation of 11.2 grms. of hæmoglobin, yielding 3.4 grms. of urea. In reality the urea in the urine was 13.4 grms. above the normal. Such an excess does not, however, tell against the formation of urea from hæmoglobin, since at this period of the experiment the increased production of blood-corpuscles tended to mask the increased destruction. That this is the explanation is rendered probable by the appearance at this time of numerous microcytes in the blood.

Day of Exper.	Urine in c.cs.	Sp. G.	Urea in grms.	Hæmocytcs per c.mm.	Weight in kilos.	Remarks.
1	{ 660	1011	7·820		13·607	
2	{ 660	1011	7·820			
3	700	1009	7·280			
4	750	1009	8·050			
5	680	1010	7·338			
6	720	1010	7·920	7,866,000		
7	620	1011	7·068	7,850,000		
8	720	1013	9·144			
9	560	1015	10·168	7,520,000		2 grm. pyrogallie acid. 1·5 grm. pyrogallie acid. Urine dark, some albumin. No bile pigments.
10	675	1018	15·380	5,195,000		Urine contains abundant albu- min and hæmoglobin. No corpuscles, no bile pigments.
11	380	1034	18·534	2,604,000		Urine contains much hæmoglo- bin, but no corpuscles. Dog takes food but is markedly icteric.
12	680	1033	21·312	1,876,000		Urine bloody. Dog is dull. Vomited matter richly bile stained; jaundice less marked.
13	360	1032	15·954	1,800,000	13·100	Urine contains much less alb., and is free from hæmoglobin.
14	300	1032	15·960	2,330,000		Dog took 650 cs. of milk. Urine gives a faint reaction of bile acids. Dog takes food well.
15	600	1014	10·520	2,546,000		Urine contains no blood, and a mere trace of albumin, with light tawny port wine colour.
16	570	1016	11·351	2,893,000	13·321	
17	530	1010	6·523	3,290,000		
18	570	1010	6·615	3,456,000		Urine free from albumin.
19	530	1011	6·042	3,630,000		
20	510	1014	6·646	4,616,000		
21	600	1011	5·360	4,935,000		
22	500	1013	6·090	4,400,000		
23	580	1012	6·460	5,606,000		
24	610	1010	6·100	5,320,000	11·70	
25	300	1030	7·778	5,220,000		
26	None.	{ 13·048	{ 13·048	4,555,000		6 grms. salicylate of soda.
27	450	1040	{ 13·048	5,105,000		6 grms. salicylate of soda. Urine dark colour, contains a trace of albumin, but no hæmoglobin. Dog appears ill, so experiment stopped.

I here introduce an experiment on the action of salicylate of soda on the blood-corpuscles and urea production. At a later part of this paper I shall enter more fully into the hæmocytic action of this drug. This experiment is not so satisfactory as the two former, because at the time the dog was recovering from the anæmia produced by pyrogallie acid, and blood-production was greatly in excess of destruction. Nevertheless, the effect of the destruction of blood on the first two days of the experiment was well marked, though on the third day the urea produced was not connected with any apparent fall in the corpuscles—in all probability because here again increased production completely masked the process of disintegration.



Exp. IV. and V.—Influence of pyrogallie acid and salicylate of soda on urea production and a number of hemocytes. 2 grms. given at *a*, and 1.5 grms. given at *b*. At *a'* 6 grms. of salicylate of soda were given, and a similar dose was administered at *b'*.

Exp. V.—SALICYLATE OF SODA.

This experiment is merely a continuation of Exp. IV. From the 17th to the 25th day the average excretion of urea was 6.303 grms. per diem. From the 13th to the 24th the corpuscles had increased at the average rate of 354,400 per c.mm. per diem. Thus if no increased destruction had been induced they would have reached 5,774,000 on the 25th day, 6,028,800 on the 26th, and 6,883,000 on the 27th.

We may therefore consider that upon the 25th a fall of corpuscles from 5,674,000 to 5,200,000 occurred. Now, calculating from our previous data, and allowing for the loss of weight in the dog, we see that such a fall will set free 8·3 grms. of hæmoglobin, which will correspond to 2·5 grms. of urea. In reality the excess over the normal on this day was 1·424 grms. of urea.

Next day the fall in the number of corpuscles must be calculated at from $5,200,000 + 354,400 = 5,554,400$ to 4,555,000, which will yield 15·7 grms. of hæmoglobin, equivalent to 4·757 grms. of urea; but this even with the surplus 1·076 grms. of the previous day falls short of the actual increased production by 0·911 grms. As is probably indicated by the marked increase on the next day, when the corpuscles, in spite of the presence of the drug in the system,—as demonstrated by its appearance in the urine,—rose from 4,555,000 to 5,105,000, the increased production was already tending to mask the amount of destruction. On the next day it is impossible to say whether or not any destruction occurred, since a rise instead of a fall in the number of hæmocytcs was noted.

We thus see that both the secretion of bile and the production of urea depend in large measure upon the destruction of blood-corpuscles, and that through this they necessarily bear a direct relationship to one another.

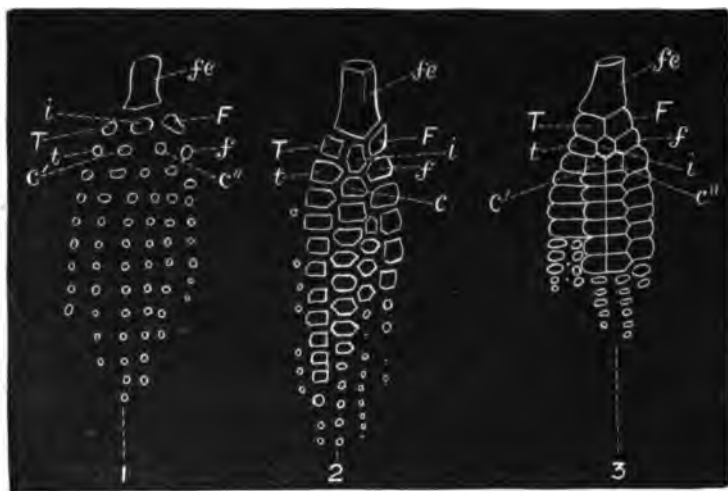
In confirmation of these conclusions, I shall, in the next place, give the results of a series of observations on the action on the red blood-corpuscles of some of the more important cholagogues which I have already shown increase the urea production.

(To be continued.)

ON THE HIND-LIMB OF ICHTHYOSAURUS, AND ON
THE MORPHOLOGY OF VERTEBRATE LIMBS. By
D'ARCY W. THOMPSON, B.A., *Professor of Biology in Univer-*
*sity College, Dundee.*¹

I AM indebted to Professor Turner for the opportunity of studying a remarkable skeleton ascribed to *Ichthyosaurus platyodon* in the Anatomical Museum of Edinburgh University. The interest of this specimen centres in the hind-limb, which presents several exceptional features. In the first place, the femur has articulated with it three bones, identifiable as tibia, intermedium, and fibula, as in Marsh's *Sauranodon* (*Baptanodon*), and as in the limb figured as *Pliosaurus portlandicus* by Owen (*Fossil*

Fig. 1.



1. Hind-limb of *Sauranodon* (after Marsh). 2. Left hind-limb of *Ichthyosaurus platyodon*. 3. Typical hind-limb of *Ichthyosaurus* (after Hulke). *fe*, femur; *T.F.*, tibia and fibula; *t. f.*, tibiale, fibulare; *i.*, intermedium; *c, c', c''*, centralia.

Reptiles), but ascribed to *Plesiosaurus Manseli* by Hulke (*Q.J.G.S.*, 1883, *Suppl.*, p. 52).² This, therefore, is an additional

¹ The substance of this paper was communicated to the British Association at Aberdeen, in August 1886.

² Long ago Buckland, in his Bridgewater Treatise, figured *I. platyodon* with three elements in the proximal tarsal row; but the circumstance passed unnoticed.

proof that the primary location of the intermedium is in the propodial segment of the limb. So far the Edinburgh specimen is only equally archaic with the American *Sauranodon*, but in the following feature it surpasses it in primitiveness.

The limb of *Sauranodon* contains in its next segment four bones, and so probably, to judge from its articular surfaces, did that of *Pliosaurus*. That is to say, granted that the bones already mentioned are rightly identified, we have in the proximal segment of the tarsus a *tibiale*, a *fibulare*, and *two centralia*. In the Edinburgh *Ichthyosaurus* we have *one centrale* only; and, moreover, we have again in the next succeeding segment *three* bones only (*tarsalia*), whereas we have five in the corresponding region of Marsh's *Sauranodon*.

So far then we have three longitudinal series of bones in perfect symmetry, formed of three bones in the propodium, three in the proximal region of the tarsus, and three in the distal. And these three longitudinal rows continue distinct to the distal extremity of the limb. Two other longitudinal series of bones exist; one, a somewhat irregular series of rounded discoid ossicles, separate from one another and without articular facets, is applied to the tibial side of the limb, commencing immediately distal to the tarsus but not directly articulated with it; the other, commencing at the same level, is inserted between the median and the external or fibular row.

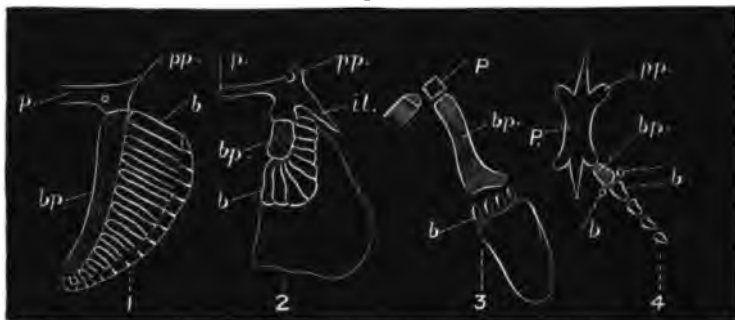
The appearance of the limb suggests at once that both of these rows are accessory and not primitive. If we may consider the ground-plan of the limb apart from them, we have simply three segmented rays or longitudinal series of bones symmetrically articulated with a basal segment.

While the limb of *Sauranodon* seemed to be a weighty argument in support of Gegenbaur's theory of the primarily double nature of the *centrale*, the present example seems to me a still more potent argument against it; for the common type of *Ichthyosaurian* limb must be considered intermediate between that of the present example and the typical cheiropterygium of the higher vertebrates; and we pass from our present case to the typical *Ichthyosaurus*, by transverse cleavage of the *centrale* and apportionment of its outer moiety to the interstitial digit.

It is perhaps equally easy to pass downwards from this limb to

the fin of fishes. Assuming the femur to represent the basipterygium: (Balfour), we have here three *basalia*, which by elongation and segmentation may be supposed to have given rise to the distal portion of the fin.

Fig. 2.



Pelvis and hind-limb of Fishes. 1. Scyllium; 2. Callorhynchus; 3. Polypterus; 4. Protopterus. *p.*, pubis; *pp.*, pre-pubic process; *il.*, ilium; *bp.*, basipterygium; *b.*, basalia.

And the limb has a close *parallel* resemblance to that of Polypterus, which is derivable by similar processes (with contemporaneous degeneration of the pelvis) from the Elasmobranch limb. In Polypterus (where I concur with Davidoff that the bone commonly called *pelvis* is actually the basipterygium) the basalia are reduced to four, or as in one specimen which I have dissected, actually to three.

It need hardly be said that this new conception of the Enaliosaurian limb is wholly incompatible with Gegenbaur's view. For Gegenbaur looks upon the whole radial (tibial) side of the Enaliosaurian or higher vertebrate limb, beginning with and including the humerus, as homologous with the basal series of the Selachian metapterygium (=basipterygium), the other elements of the limb being attached laterally to the base, on the ulnar (fibular) side. While on the present view, the humerus (femur) is the only basal representative, and to it are attached radial, ulnar, and intermedial rays.

It remains to be seen whether an explanation can be found for the Dipnoan limb, which has remained unexplained since the view became untenable that it was superlatively archaic. In the fin of Protopterus, the segment articulating with the pelvis is, I take it, a true basipterygium. To it I have found

attached two small nodules of cartilage, between which is the main axis of the fin. Here we seem to have three basalia, two aborted, and one only continued into a segmented ray, as are all in our *Ichthyosaurus*. While in *Ceratodus*, we are reduced to supposing that this one segmented ray has branched laterally, in order to give breadth and strength to the fin.

In the fore-limb of the Edinburgh *Ichthyosaurus*, the intermedium no longer articulates with the humerus, and the centrale is already double; so that here we have, as usual, a marked preponderance of archaic features in the hind as compared with the fore-limb.

Editorial Note.—This specimen of *Ichthyosaurus* from Lyme Regis, Dorsetshire, was at one time the property of Sir William Jardine, Bart., of Applegarth. It was purchased at the sale of his scientific collection by Professor Archibald Geikie for the University of Edinburgh, and is now displayed in the vestibule of the Anatomical Museum in the New Buildings of the Medical School.—W. T.

THE LUMBAR CURVE OF THE SPINAL COLUMN IN
SEVERAL RACES OF MEN. By Professor Sir WILLIAM
TURNER, M.B., LL.D., F.R.S.

IN the course of the investigations into the modifications of the skeleton in different races of men, which I have been conducting in connection with my Report on the Human Skeleton for the Reports of H.M.S. "Challenger," I have measured the bodies of the lumbar vertebræ, with the view of ascertaining if modifications existed in their vertical diameter, anteriorly and posteriorly, which might affect the lumbar curve of the spine. If the vertical diameter of the series of lumbar bodies be less anteriorly than posteriorly, then the lumbar region possesses (if this be not compensated for by modifications in the thickness of the intervertebral discs) an anterior concavity, continuous with the anterior concavity in the dorsal region; and an approximation to the curvature of the spine is produced, such as is characteristic of the spinal column in all mammals except man.

Anatomists are in the habit of teaching that the human spine is convex forward in the lumbar region, so that a lumbar convexity is interposed between the thoracic and sacral concavities, and contributes to the alternating series of concavo-convex curves of the spinal column, which are associated with the erect attitude of man. My belief in the universality of the view that the human spine is invariably convex forward in the lumbar region was disturbed some years ago, when Charles Robertson, Esq., of the Oxford Museum, showed me the skeleton of an aboriginal Australian in that museum, which he had articulated in 1873. Mr Robertson told me that the skeleton was that of an adult male of the Tomki tribe of the Richmond River, N.S.W. In it there was a continuous curve, concave forwards through both thoracic and lumbar regions. As the skeleton was, however, artificially articulated, the question naturally arose in one's mind if this modification in the lumbar curve might not have been produced by some peculiarity in the method of articulation, and was not therefore natural to the spine. Since I saw this skeleton, however, Mr Robertson has written to tell me of another adult male from Port Augusta, South Australia,

articulated in 1878, which exhibited a similar concavity in the lumbar region, and that the articulated skeletons of a Gilbert Islander and a male Andaman Islander have a similar lumbar concavity, though not so well marked. Before I had heard, however, of these later specimens in the Oxford Museum, I had examined the lumbar vertebræ in the series of spines at my disposal, and had obtained some interesting results.

Two important factors contribute to the curve in the lumbar region, viz., the vertebral bodies and the intervertebral discs. The exact share contributed by each of these parts can only be ascertained with precision by the method of observation which Professor D. J. Cunningham, of Trinity College, Dublin, is conducting, of making longitudinal mesial sections through the long axis of the spine in frozen subjects, and then carefully measuring the relative thickness both of the vertebral bodies and the discs. In the absence, however, of the fresh bodies of Australians and other aborigines, I have been precluded from obtaining any information on the thickness of the discs, and have been restricted to the examination of the vertebræ themselves, so far as they have been preserved in the skeletons which have reached me. I have measured, therefore, the vertical diameter of the body of each lumbar vertebra, both in front and behind, and have noted the difference in each vertebra, and in the series of lumbar vertebræ in each spine.

In order to obtain some data for comparison I measured the lumbar vertebræ in twelve adult European spines, the majority of which were males, and found that the vertical diameter of the anterior surface of the bodies of the five vertebræ in each spine was collectively greater than the vertical diameter of the posterior surfaces in the same spine. The maximum difference between the collective depth of these surfaces in the series of five vertebræ was 11 mm. in one skeleton, and the minimum difference was 1 mm. in another skeleton. The mean collective depth of the five vertebræ in the twelve European skeletons was 137 mm. for the anterior, and 131.4 for the posterior surface, the mean difference therefore was 5.6 mm. in favour of the anterior surface. If we were to assume that in these spines each intervertebral disc was of equal thickness throughout, then the greater thickness of the vertical diameter of the bodies in front than behind in each spine would give a slight convexity forwards to the spinal column in the lumbar region. But there is reason to believe that this difference in vertical diameter is not limited to the vertebral bodies, and that some of the discs also are thicker anteriorly than posteriorly so as to increase the anterior convexity.

If we now examine the individual lumbar vertebræ in each of these European spines we shall find that with only two exceptions the body of the 1st lumbar vertebra was deeper behind than in front, in one instance 6 mm., in another 4 mm. but usually not more than 1 or 2 mm.; in the exceptional cases the anterior and posterior vertical diameters were equal. The body of the 2nd lumbar was deeper behind than in front in six spines; they were equal in depth in four spines, and the anterior surface was deeper than the posterior in two spines. The body of the 3rd lumbar was deeper in front than behind in ten spines, and in two they were equal. The body of the 4th lumbar was deeper in front than behind in eleven spines, and deeper behind than in front in one specimen. The body of the 5th lumbar was deeper in front than behind in all the specimens. From these spines it is evident that, whilst in the 1st and 2nd lumbar vertebræ the body was deeper behind than in front in a considerable proportion of the specimens, in the 3rd and 4th lumbar the reverse occurred, until in the 5th lumbar the bodies of all the specimens had a greater vertical diameter anteriorly than posteriorly, and this indeed is a character of the 5th lumbar that has long been recognised by the descriptive human anatomist. In this series of twelve European spines, if we take the vertical diameter of the body of the 4th lumbar in the series we find that it amounts to 336 mm. for the anterior surfaces collectively, and to 313 mm. for the posterior surfaces collectively. In the 5th lumbar the vertical diameter of the anterior surfaces collectively amounted to 337 mm. and the posterior surfaces to 281 mm.; the mean anterior depth was 28 mm., the mean posterior 23·4, and the mean difference in favour of the anterior surface was 4·6 mm. Hence it follows that of all the lumbar vertebræ the 5th has much the greatest proportional depth at the front than at the back of its body, and that it contributes more than any of the others to the anterior convexity of the lumbar portion of the spinal column.

For the purposes of comparison of the lumbar region in Europeans with that in the spines of other races of men, it may be well to frame a lumbar index both for the entire region and for the body of the 5th lumbar. If we assume the vertical diameter of the bodies of the five vertebræ anteriorly to = 100, then the formula
$$\frac{\text{posterior diameter} \times 100}{\text{anterior diameter}}$$
 would give the index required. If this be applied to the lumbar region in Europeans the mean index in them of the series of five vertebræ is 95, and the mean index of the 5th lumbar vertebra itself is 83.

During the past few years I have collected the skeletons of seven adult aboriginal Australians,—six men and one woman. In four of the men the lumbar spine is complete, in one the last lumbar vertebra has been lost, in another the 3rd, 4th, and 5th lumbar are absent; in the woman all the lumbar are present. In each of the five skeletons in

which the lumbar spine was complete, the vertical diameter of the bodies of the five vertebræ collectively was deeper behind than in front; the maximum difference observed in three male skeletons was 9 mm., the minimum in the woman was 2 mm. The mean collective depth of the five vertebræ in the five perfect Australian skeletons was 112.2 mm. for the anterior surface of the bodies, and 118.8 mm. for the posterior surface; the mean difference, therefore, was 6.6 mm. in favour of the posterior surface. In the relation of the vertical diameter of the posterior surface to the anterior surface the opposite condition prevailed to that which was found in the Europeans. In the skeleton in which the 5th lumbar was absent the collective diameter of the four lumbar was 3 mm. greater behind than in front. Before, indeed, I had measured the vertebræ in these Australians, I found that, when the lumbar in each spine were articulated together, the bodies gave a concave curve forward, and not a convex curve as in the European spine, so that I was not surprised to see, when the bodies were measured, that collectively they were deeper posteriorly than anteriorly.

When the measurements of the individual lumbar vertebræ in the series of Australian spines were examined, it was seen that the body of the 1st lumbar vertebra in every instance was deeper behind than in front, in four skeletons as much as 4 mm. The body of the 2nd lumbar was with one exception deeper behind than in front, in two specimens as much as 4 mm.; in the exceptional vertebra the depth in front was 1 mm. greater than behind. The body of the 3rd lumbar in four skeletons was deeper behind than in front; in one skeleton they were equal, and in another—the adult female—the anterior diameter was 1 mm. deeper than the posterior. The body of the 4th lumbar was deeper behind than in front in three skeletons; these diameters were equal in one, and in two the anterior diameter was greater than the posterior. The body of the 5th lumbar was deeper in front than behind in all the five complete skeletons, the maximum difference between the two surfaces being 3 mm.

When these dimensions are compared with those obtained from the European spines, it will be seen that in the 1st, 2nd, and 3rd lumbar the body was more constantly deeper behind than in front in the Australians than in the Europeans. In the 4th lumbar, whilst it was the exception in the Europeans for the body to be deeper behind than in front, in the Australians one-half the skeletons exhibited this relation. In all the Australians, as in the Europeans, the body of the 5th lumbar was deeper in front than behind; the mean vertical diameter of the anterior surfaces was 23.2, and of the posterior 21.2, a difference of 2 mm. only in favour of the anterior surface; whilst in the Europeans the anterior surface was on the average 4.6 mm. thicker than the posterior.

The mean lumbar index in the Australians was 105.8, and the mean index of the 5th lumbar vertebra was 91.

In my single male Bush skeleton the collective vertical diameter of the bodies of the five lumbar vertebræ was 108 mm. anteriorly, and 115 mm. posteriorly. In the 1st, 2nd, and 3rd lumbar the posterior diameter exceeded the anterior; in the 4th these two diameters were equal, and in the 5th the anterior diameter was 1 mm. greater than

the posterior. The proportions in this skeleton closely corresponded to what was seen in the Australians. The lumbar index was 106, and the index of the 5th lumbar vertebra was 95.

In my series of Andamanese skeletons only two had the lumbar vertebræ completa. In one the vertical diameter of the five vertebræ collectively was 113 mm. anteriorly, and 112 mm. posteriorly; in the other 125 mm. anteriorly, 124 mm. posteriorly. The 1st and 2nd lumbar in both skeletons were thicker behind than in front. The 3rd lumbar in one skeleton was of equal diameter on both aspects, and in the other was 1 mm. thicker behind than in front. In both skeletons both the 4th and 5th lumbar were thicker in front than behind, in the one skeleton the anterior surface of the 5th lumbar being 3 mm., in the other 5 mm., thicker than the posterior. The mean lumbar index of the two skeletons was 99, and the mean index of the 5th lumbar vertebra was 84.

In three Negro skeletons I was able to measure the vertical diameter of the bodies of the lumbar vertebræ both in front and behind. In each of the three skeletons the collective vertical diameter of the five lumbar bodies was slightly greater in front than behind; the maximum difference, however, was only 2 mm. The mean collective depth of the five vertebræ in the three Negro skeletons was 121 mm. for the anterior surfaces, and 119.6 mm. for the posterior surfaces; the mean difference, therefore, was 1.4 mm. in favour of the anterior surface. In all three skeletons, both the 1st and 2nd lumbar were slightly deeper behind than in front; the 3rd lumbar was equal in depth both anteriorly and posteriorly, whilst both the 4th and 5th lumbar were somewhat deeper in front than behind. The mean lumbar index was 98.9, and the mean index of the 5th lumbar vertebra was 89.

In a Maori skeleton, from Otago, the vertical diameter of the series of five vertebræ, was the same both in front and behind, viz., 101 mm. The 1st and 2nd lumbar were slightly deeper behind than in front, the 3rd and 4th were equal in depth on both surfaces, and the 5th was 3 mm. deeper in front than behind. The lumbar index was 100, and the index of the 5th lumbar vertebra was 85.

In each of two female skeletons from Oahu, in the Sandwich Islands, the collective vertical diameter of the five lumbar bodies was greater behind than in front; in the one skeleton the difference was 7 mm., in the other 4 mm., in favour of the posterior surface. The mean collective depth of the five vertebræ in the two skeletons was 117.5 mm. for the anterior and 123 mm. for the posterior surfaces; the mean difference, therefore, was 5.5 mm. in favour of the posterior surface. In both skeletons the bodies of the 1st, 2nd, 3rd, and 4th lumbar were all deeper behind than in front, whilst the 5th lumbar was deeper in front than behind. The mean lumbar index was 104.7, and the mean index of the 5th lumbar vertebra was 87.

In one of three Hindoo skeletons, a tall male,¹ the vertical diameter of the series of five lumbar bodies was 137 mm. anteriorly, and 146 mm. posteriorly. The 1st, 2nd, and 5th lumbar were deeper behind

¹ This skeleton, presented by Dr John Anderson, F.R.S., was estimated as belonging to a man 6 feet high.

than in front, the 3rd was 1 mm. deeper in front than behind, and in the 4th these two diameters were equal. The lumbar index was 106, and the index of the 5th lumbar vertebra 107. In the two other Hindoo skeletons, a male and a female, the vertical diameter of the bodies of the five lumbar was somewhat deeper in front than behind, and the mean lumbar index was 97·8. In each of these skeletons the vertical diameter of the 5th lumbar vertebra was deeper in front than behind, and the mean index was 89. In the skeleton of a male Sikh, the vertical diameter of the five lumbar bodies was 130 mm. anteriorly and 133 mm. posteriorly, being a difference of 3 mm. in favour of the posterior diameter. In this skeleton the 1st and 5th lumbar bodies were deeper behind than in front, but the 2nd, 3rd, and 4th were each of equal diameter on both aspects. The lumbar index was 102, and the index of the 5th lumbar vertebra was 108·7.

In a Chinese skeleton the vertical diameter of the five lumbar bodies was 145 mm. anteriorly, and 123 mm. posteriorly. In each vertebra, except the 1st, the vertical diameter was deeper in front than behind, and in the 1st the two diameters were equal. The lumbar index was 84·8, and the index of the 5th lumbar vertebra was 70. In a male Malay skeleton, the vertical diameter of the five lumbar bodies was 127 mm. anteriorly, and 125 mm. posteriorly. In the 1st, 2nd, and 3rd, the posterior diameter was deeper than the anterior; in the 4th and 5th the anterior diameter was deeper than the posterior. The lumbar index was 98, and the index of the 5th lumbar vertebra was 77·7.

In a female Esquimaux, the vertical diameter of the series of five lumbar bodies was the same in front and behind (127 mm.), so that the lumbar index was 100. In a male skeleton the vertical diameter of the bodies anteriorly was 120 mm., and posteriorly 116 mm., and the lumbar index was 96·6. Both in the female and male the 1st and 2nd lumbar were deeper behind than in front, but the 4th and 5th lumbar were deeper in front than behind. The index of the 5th lumbar vertebra in the female was 81, and in the male 71. In a male Laplander the vertical diameter of the five lumbar vertebræ was 111 anteriorly and 110 posteriorly, and the lumbar index was 99. In a female Laplander the vertical diameter was anteriorly 121 mm., and posteriorly 118 mm. and the lumbar index was 97·5. In both skeletons, whilst the 1st lumbar vertebra was deeper behind than in front, both the 4th and 5th lumbar were deeper in front than behind. The index of the 5th lumbar in the male was 86, and in the female 88.

From the data which are recorded in the preceding pages of the measurements of the lumbar region in thirty-six spines of various races of men, it will be seen that differences occur, often to a considerable degree, in the vertical diameter anteriorly and posteriorly of the bodies of the series of five vertebræ. These differences are expressed numerically by the lumbar index, computed in the manner already explained. The lowest index (84·8) was in a

Chinese skeleton, and the highest (106) in a Bushman and in a male Hindoo, with a mean of 105·8 in a series of five Australians, whilst the mean index of twelve Europeans was 95. The number of Europeans measured may, I think, be regarded as sufficient on which to frame an average. But it would not be safe to speak so definitely of the mean index in the other races, on account of the few skeletons which have as yet been measured. Still, from the fact that each of the five Australian skeletons presented the character of having the vertical diameter of the series of lumbar bodies deeper posteriorly than anteriorly, and from the peculiarities of the two Australian skeletons in the Oxford Museum articulated by Mr Charles Robertson, there can, I think, be little doubt that in that race it is the rule for the lumbar vertebræ to have an opposite relation, as regards the depth of the body, to what is found in Europeans.

So far then as one can judge of the configuration of the lumbar spine by the measurements of the bodies of the vertebræ without the intervertebral discs, this region may present one or other of three forms in different races of men. It may be convex forwards; or straight; or concave forwards, and to each group a numerical limit may be assigned, based on the lumbar index. We may assume that a spine with the lumbar index from 98 to 102, both inclusive, is a straight spine, *Ortho-rachic*; one with an index above 102 is a spine concave forwards, *Koilo-rachic*; and one with an index below 98 is a spine convex forwards *Kurto-rachic*. From the data before me the skeletons which I have measured would be arranged as follows:—The Chinese and Europeans would have convex lumbar regions, the Andamanese, Negros, Maoris, Sikhs, and perhaps Hindoos, Esquimaux, and Lapps would have straight lumbar regions, whilst the Australians, Bush, and Sandwich Islanders would have concave lumbar regions. But this arrangement is of course entirely provisional and will doubtless require to be modified as observations on the lumbar vertebræ are multiplied. Variations in the anterior curvature of the spine in the lumbar region would in all probability affect the outline of the back of the body in the lumbar region, as one would not expect the back to have so well marked a hollow in that region, when the spine is concave forwards as when it possesses the anterior convexity. How far these depart-

ures in the lower races of men from the well-recognised lumbar convexity of the higher races may serve to modify the spine in the erect attitude can only be definitely settled when the intervertebral discs, as well as the vertebral bodies, have been measured.

As regards the 5th lumbar vertebra, in all the races the vertical diameter of the anterior surface of the body is deeper than that of the posterior. There are without doubt differences in the relative depth. The anterior diameter is proportionally greater than the posterior in the Chinese, Malay, Esquimaux, Lapps, Europeans, and Andamanese, than in the Australians, Bush, Negros, and Hindoos. In one Hindoo skeleton, and in the Sikh, the posterior diameter of this vertebra was deeper than the anterior, but these were probably individual exceptions, and this greater depth would assist in giving the high lumbar index exhibited by these two skeletons.

Anatomical Notices.

FLOATING KIDNEY. By W. ARBUTHNOT LANE, M.S.

IN a female subject in the dissecting room I found the right kidney freely movable. It was completely enclosed in peritoneum, and was attached to the abdominal wall by a mesentery, whose attachment to the kidney extended from the upper extremity of its inner margin to the lower limit of the hilum. This mesentery was connected to the abdominal wall in a direction extending obliquely downwards and to the right from the origin of the right renal artery from the aorta. The mesentery at its attachment to the abdominal wall was $4\frac{1}{2}$ inches in breadth. The renal artery and vein ran along its free inner margin, which was $3\frac{1}{2}$ inches long, its outer margin measuring $2\frac{1}{2}$ inches. The ureter, which was lax and tortuous, ran up behind the kidney, where it passed between the two layers of the mesentery, and expanded to form the pelvis. The kidney was placed obliquely, its direction being downwards and to the left. It was considerably smaller than the left kidney, and had a cyst in its anterior wall $\frac{3}{4}$ of an inch in diameter. The right suprarenal capsule occupied its normal position. The kidney could be easily made to lie on the left side of the spinal column, and to reach the front and left side of the fifth lumbar vertebra and the lumbo-sacral articulation. The left kidney was more extensively covered by peritoneum than usual. The liver and spleen were not enlarged. The woman was not very stout, but her tissues were soft and flabby. Her vessels were all remarkably tortuous. She had worked hard, as her spinal column showed well-marked pressure changes. In this specimen the kidney possessed a more complete peritoneal investment than in the case described by David Hepburn, M.B., in the *Journal of Anatomy and Physiology*, Jan. 1885.

AN INTERCLAVICULAR MUSCLE IN THE HUMAN SUBJECT. By W. ARBUTHNOT LANE, M.S.

I FOUND the following remarkable muscle in the body of a powerfully-built male subject. It consisted of two symmetrical fleshy bellies of considerable size. These were joined by a round tendon nearly as

thick as that of the long head of the biceps muscle. Each fleshy belly arose from the clavicle immediately in front of the attachment of the rhomboid ligament, and from the front of the rhomboid ligament just below its clavicular insertion. The muscle measured $1\frac{1}{2}$ inch in transverse measurement at its origin. Its tendon crossed the front of the manubrium nearer its lower than its upper limit, but it was in no way connected to it. On the front of the manubrium, on each side of the middle line, it was joined by a rounded tendon. This tendon, which was not an aponeurotic expansion, was derived from the upper part of the sternal portion of the pectoralis major; namely, that portion which usually arises from the manubrium sterni and the inner portion of the first costal cartilage. In this case this part of the muscle had no insertion into bone or cartilage, but ended in a tendon, which passed freely over the sternum, and fused with the tendon of the digastric interclavicular muscle. The portion of the pectoralis major below this, and the clavicular division of the muscle, had their usual attachments. The latter covered a great part of each belly of the interclavicular muscle, and between it and the upper portion of the sternal division of the muscle there was an angular interval of considerable size, in which the belly of the interclavicular muscle appeared. The interclavicular muscle had no connection with the subclavius, from which it was separated by the costo-coracoid membrane. Its function was evidently to approximate the clavicles. That portion of the pectoralis major joining it formed practically an interhumeral digastric muscle. It could be separated as a distinct muscle from the remainder of the pectoralis major for a very considerable distance. The subclavius, costo-coracoid membrane, rhomboid, and coraco-clavicular ligaments were normal.

This variety in the supernumerary muscles attached to the clavicle is rare, and the nearest approach to the form above described is one named by Professor Gruber, *musc. interclavicularis anticus digastricus*, and described by him in *Reichert u. du Bois-Reymond's Archiv.*, 1865, vol. vii. p. 710, pl. xviii. fig. 3.

Notices of New Books.

Revue d'Anthropologie, Dirigée par Paul Topinard, Troisième Série,
Tome i., Premier Fascicule. Paris, 1886.

IN 1872 the late M. Paul Broca founded the *Revue d'Anthropologie*, and up to the time of his much lamented death was actively engaged both in writing for it and in editing it. At his death the direction of the *Revue* was intrusted to M. Topinard, Secretary of the Anthropological Society of Paris. From its foundation it has been the recognised medium for the publication of a number of valuable memoirs in the French language on various branches of anthropology. With the commencement of the present year a new series, the third, of the *Revue* is begun, under the direction of M. Topinard, whose recent most elaborate work, entitled *Éléments d'Anthropologie Générale*, has placed him in the first rank of living anthropologists. Co-operating with him in the direction are such well-known names as MM. de Quatrefages, Hamy, Mathias Duval, General Faidherbe, Dr Gavarret, the Marquis de Nadaillac, Baron Larrey, MM. Jules Rochard, L. Rousset, and d'Arbois de Jubainville.

The number for January contains original articles by Dr Topinard, Dr Verneau, M. Seeland, M. de Nadaillac, and M. Ledouble. In addition, there are critical and prehistoric reviews, and abstracts of various memoirs from the German, English, and French.

Report of a Committee of the Clinical Society of London, nominated
November 10, 1882, to investigate Spina Bifida and its Treatment
by the Injection of Dr Hunter's Iodo-Glycerine Solution.

THIS report, which has been lately issued, bears the signatures of Howard Marsh, A. Pearce Gould, H. H. Clutton, and R. W. Parker, hon. sec. Before attempting to discuss the results of the treatment, the committee thought it of essential importance to determine, more clearly than had hitherto been done, the pathological conditions included under this term, and with that object undertook examination of all the specimens contained in London museums, as well as those in Cambridge and Glasgow, amounting to 125. They thus went over much the same ground as I had done, and their conclusions are, in the main, confirmatory of the conclusions given by me in the *Lancet*, March 25, 1885, and in vol. xix. of this *Journal*,—viz., (1) the spinal cord and nerves are, in most cases, prolonged into the sac, and expanded in its walls. The nerves proceed from the sac in regular order through the intervertebral foramina, some running forwards with the cord into the spinal canal; and the ganglia upon the posterior roots

are normal, though, in a few cases, as shown by specimens in the Cambridge Museum, two or more are blended together. (2) When the spina bifida is in the upper lumbar or dorsal region the cord may be traced again from the sac into the lower part of the spinal cord. (3) The arachnoid is traceable into the sac, as well as the dura mater; and the fluid is in the subarachnoid space. I conclude it is implied that the fluid is, as I have stated it to be, in the *anterior* subarachnoid tissue. (4) As a rule, the base only of the tumour is covered with skin, which ends abruptly in a thin membrane in which the various tissues, including the nervous, and the membranes of the cord, are blended. (5) The instances in which the cavity of the sac is a dilatation of the central canal of the cord are very rare. With reference to this there is the following important addition to our knowledge:—"The histology of the sac-wall in a typical case of meningo-myelocoele, by demonstrating the integrity of the central canal of the included portion of the cord, settles beyond doubt what must otherwise be matter of conjecture only, that neither does the neural furrow remain unclosed in spina bifida, nor, after having been closed, is it subsequently distended by dropsy and ruptured;" and "this examination seems to complete the refutation of the view held by Förster and many subsequent German writers, viz., that spina bifida, in the great majority of cases, is due to a dropsy of the central canal of the cord." (6) The malformation is attributable to imperfect development of the mesoblastic tissues on the posterior aspect of the cord; but the difficult question of the relation of the collection of fluid to the imperfection of development is not discussed. The fixation of the cord in the sac from an early period of embryonic life of course prevents its ascent in the spinal canal during development, and in some cases reverses the ordinary direction of the nerves, causing them to pass upwards to their intervertebral foramina instead of downwards.

The pathological anatomy of the three varieties—*Spinal meningocele* (protrusion of the membranes only), *meningo-myelocoele* (protrusion of the membranes with the cord and nerves), and *Syringo-myelocoele* (dilatation of the central canal), is said to be strictly parallel with those occurring in the head, viz., *Meningocele* and *Encephalocoele*; but by what contrivance the *three* spinal conditions are to be made to correspond with the *two* cerebral we are not told.

Though not denying the occurrence of spinal meningocele, I was not able to find a single unequivocal example of it; and I must confess to feel great doubt about some, at any rate, of the ten examples of this condition mentioned in the report.

Analyses of the fluid by Dr Halliburton show slight alkaline reaction, slight opalescence on boiling, small quantity of solid matter, consisting of sodium chloride, phosphates, and carbonates, with small fraction of proteids, which was composed of globulin.

Some unusual varieties are mentioned, such as subdivision of the sac and the presence of bony outgrowths across the spinal canal in the neighbourhood of the tumour, five examples of the latter being given.

Die Chirurgische Anatomie in ihrer Beziehung zur Chirurgischen Diagnostik, Pathologie und Therapie, ein Handbuch für Studierende und Aerzte, von Prof. Dr. MAX SCHÜLLER, in Berlin, Heft i., Die obere Extremität, 1885.

THIS promises to be the most complete and exhaustive treatise on surgical anatomy that has hitherto appeared in any country. It is illustrated by numerous woodcuts, is written in a simple style, and will be valued both by students and practitioners. It gives surface markings, measurements, disposition of fasciæ, vessels, muscles, &c., descriptions of joints, directions of dislocations and fractures, the causes of displacements, the courses which matter is likely to take, the position of aneurisms, wounds of arteries, the methods of compression and ligaturing the several arteries, re-setting joints, and a variety of information bearing upon the practice of surgery. The action of the several muscles is given, with the effects of paralysis of them, and the appropriate points for Faradization.

When fluid is injected into the shoulder-joint in the dead body the arm is said to be thereby slightly raised, abducted, and rotated inwards, the head of the humerus to be pressed a centimeter away from the glenoid cavity. At the same time the lower angle of the scapula is thrown a little backwards—this and the abduction of the arm being due to the comparative looseness of the capsule at its under part. The swelling and fluctuation are most perceptible in front and behind; and the synovial processes upon the biceps-tendon and the subscapular muscle become distended. When the cavity of the elbow-joint is in like manner filled the fore-arm becomes bent upon the arm nearly to a right angle, and semi-prone. The capsule, as shown in a woodcut (p. 198), is distended all round, but especially in front and behind on the sides of the brachialis anticus and the triceps; and the radius and ulna are found to be distanced from the humerus one or two millimetres. In the case of the radio-carpal joint the hand remains in a straight line with the fore-arm, or slight dorsal-flexion may be induced, and the articular surfaces are separated three or four millimetres from one another.

At page 309 is represented the dissection of a specimen of contraction of the palmar fascia (Dupuytren's contraction) in which the processes of the fascia extending into the fingers are seen to be thickened and contracted, while the flexor tendons, as the author remarks, are unaffected. He notes the fact that the fascial processes of the ring finger are commonly first affected, which he rightly attributes to the circumstance that pressure from a stick or other body held in the hand is most felt at this part, and acts as a source of irritation to the skin and fascia here.

Enough has been said to show that the work, in this its first instalment, is a valuable practical addition to anatomical literature.

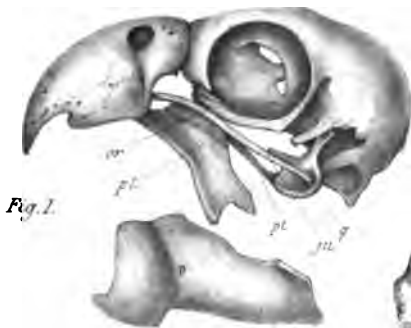


Fig. 1.



Fig. 2.

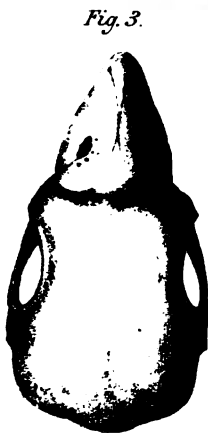


Fig. 3.

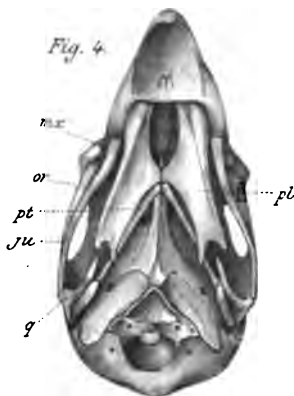


Fig. 4.

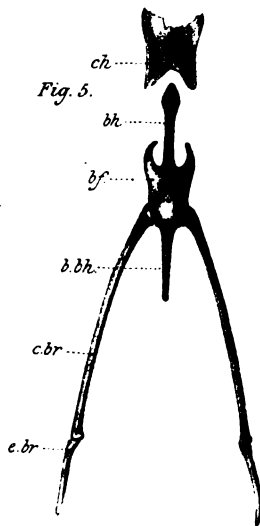


Fig. 5.

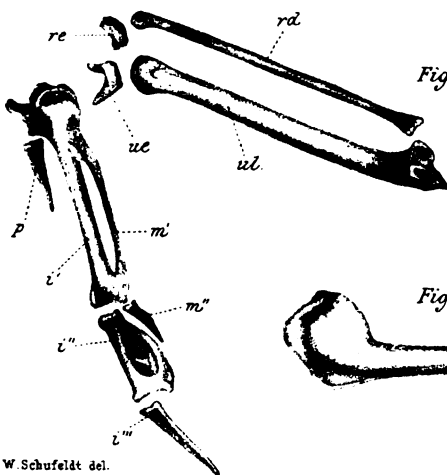


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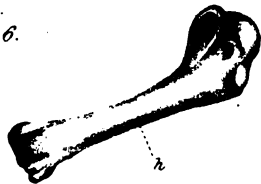


Fig. 7.

R. W. Schufeldt del.

F. Roth, Lith. Edin.



Fig. 8.

Fig. 10.



Fig. 9.



Fig. 12.

Fig. 11.



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Fig. 13.

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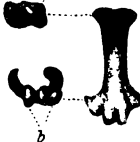


Fig. 14.



Fig. 15.

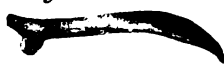


Fig. 18.



Fig. 16.

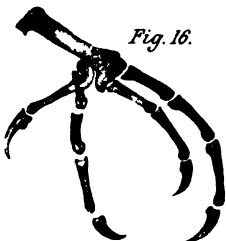
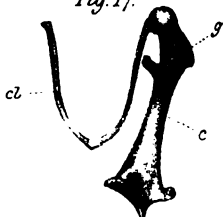


Fig. 17.



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3. The third part of the document is a list of names and titles, including "The Hon. Mr. Justice" and "The Hon. Mr. Justice".

Fig. 1.



Fig. 2.



Fig. 3.



Fig. 4.





Fig. 1.

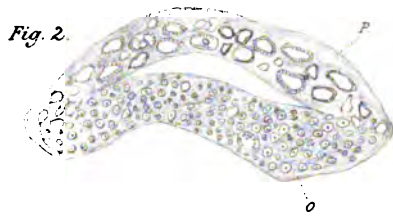


Fig. 2.

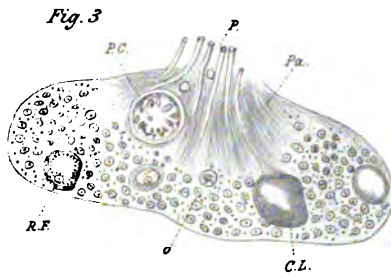


Fig. 3.

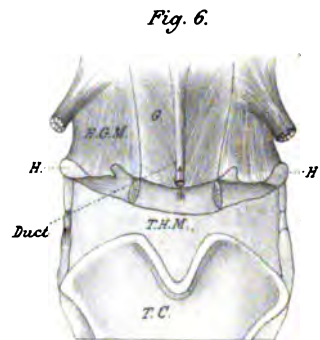


Fig. 6.

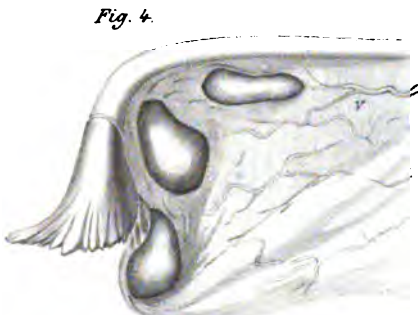
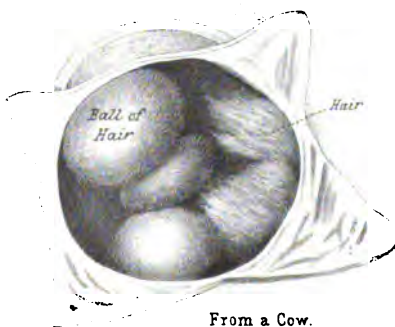


Fig. 4.

Cysts in the broad Ligament of a Mare.

Fig. 5.



From a Cow.



Trachea of Emu

Fig. 1.



Fig. 2.



BLOOD FORMING CELLS.

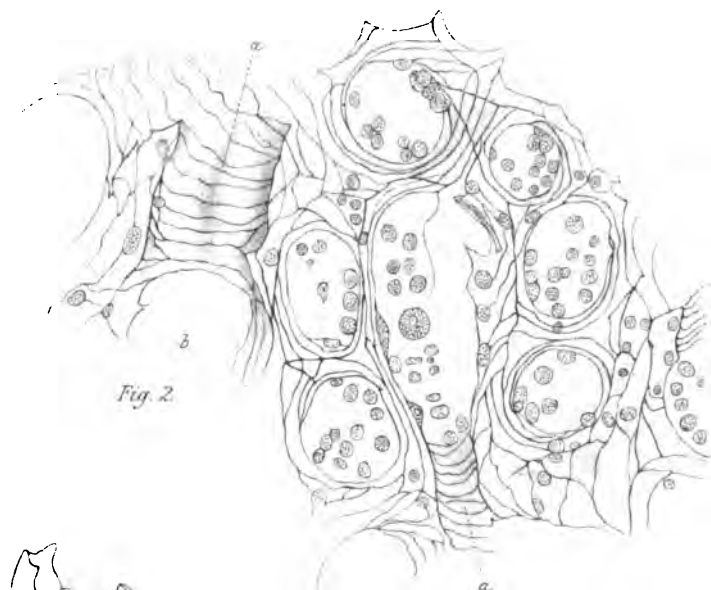


Fig. 2.



Fig. 1.



Fig. 3.

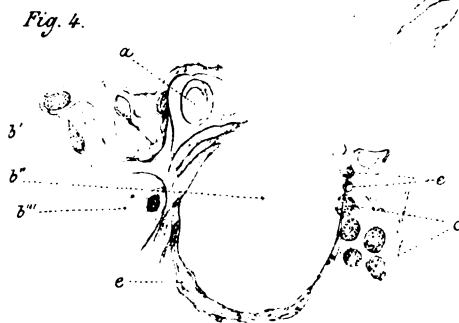


Fig. 4.



MALFORMED FROG.

From Photograph

F. HUGHES, Lith. Edin.



Journal of Anatomy and Physiology.

ON THE PHYSIOLOGY OF THE HEART OF THE ALLIGATOR. By T. WESLEY MILLS, M.A., M.D.,
Lecturer on Physiology, M'Gill University, Montreal, Canada.

THE only paper bearing on the physiology of the heart of the *Crocodylia* is one by Gaskell, in vol. v. No. 1 of the *Journal of Physiology*. The anatomy of the sympathetic is considered by this writer in a paper in Nos. 4, 5, and 6 of vol. v. of the same.

With some of the conclusions in the former short communication my observations accord; with others they are entirely at variance. I shall therefore refer in some detail to the experiments leading me to opposite conclusions from the writer referred to above.

My experiments were made upon specimens of *Alligator Mississippiensis*, part of them at the Marine Laboratory of the Johns Hopkins University at Beaufort, N.C.; and part of them in the Biological Laboratory of the same institution in Baltimore, to the directors of both of which I desire to acknowledge my indebtedness for their kindness in facilitating this work. Gaskell has stated, in the paper referred to, that in the Crocodile "the vagus seems to contain purely inhibitory fibres." That such is far from being the case, the following extract from notes of my experiments on the Alligator will amply show. It is scarcely to be supposed that the case would be different for creatures so alike as the Crocodile and the Alligator.

For stimulation the interrupted current of a Du Bois' induction coil fed by one Bunsen's cell was used.

I. The Results of Stimulation of the Vagus Nerve.

The following extracts from my notes bear on this subject:—

Experiment.—

Cardiac rhythm = 42.

1. Stimulation of right vagus with interrupted current led to arrest, and the following after-rhythm :—

During the 1st	minute	43
"	2nd	" 44
"	3rd	" 43
"	4th	" 43

After 10 minutes R. = 42.

2. Stimulation of left vagus led to arrest, and the following after-rhythm :—

During the 1st	minute	40
"	2nd	" 39
"	3rd	" 40
"	4th	" 41
"	8th	" 44

The original rhythm was 40 to 41.

In another case, in which the heart was much depressed in action and the rhythm slow, a single stimulation raised the rhythm from 10 to 17, with marked increase in the force of the beat.

I have given the exact rhythm in the above cases to show the amount of acceleration. This is quite as much as would be expected for a rate of beat so high as 40, and quite as much as occurs usually in the Chelonians.

II. How the Vagus arrests the Heart.

As in the Chelonian, a current that suffices to stop the auricle proper ("bulged" part) will not arrest the sinus or sinus extension ("basal wall") in all cases; so long as the sinus venosus continues to beat the ventricle will follow, at least while the beat is not very weak indeed.

Often a momentary stop of the ventricle follows the arrest of the auricles, but it is very short in such cases.

Practically, as in the Chelonians, the sinus is the controlling part of the heart so far as rhythm is concerned; when it is arrested the auricles or ventricle ceases to pulsate.

As to whether the arrest is due solely to the influence of the vagus in the sinus is considered in my paper on the Sea-Turtle.

Sometimes, in consequence of this greater power of the vagus over the auricles, a very weak current will produce, when first

applied, an arrest of both auricles and ventricle of brief duration, when the continuance of the stimulation will give rise not to arrest but to acceleration; that is, the auricle breaks away and participates in the good effects of vagus-stimulation exactly as if the current had been withdrawn. As in the Chelonians, the heart is arrested promptly by the vagus, and not by reducing the force of the beat to zero.

After-Effects of Stimulation of the Vagus.—These vary with a variety of circumstances, and follow much the same laws as in the Chelonians.

2. When the rhythm at the time of stimulation is rapid, the after-rhythm is not much in advance of the original; it may for some time even fall slightly below it, but if the rhythm be very slow the proportionate increase may be very great.

2. But in all cases there is an increase in the force of the beat, seen in ventricles as well as auricles. This is best noted when the original beat is feeble, or when one beat is of force disproportionate to another. In the Alligator this increase of the strength of the beat has been the most striking phenomenon.

3. Stimulation of the vagus removes irregularities both in the force and frequency of the beat; this follows, not only when the heart is slightly disturbed, but when its whole action is very much depressed.

4. The arrest of the beat usually follows after a very brief period of latency; and after the cessation of stimulation the beat recommences after a latency which varies with the condition of the heart. When this organ is strong, and at an early stage of experimentation, the latency last referred to is usually from three to five seconds; but later this may be doubled or trebled.

5. The acceleration that follows vagus-stimulation reaches its maximum sooner, and declines more speedily when the heart's nutrition has begun to suffer than when the heart is fresh. The difference in this respect is very great; often the maximum acceleration is reached under bad conditions of nutrition in one minute, while in a fresh condition of the heart the maximum of acceleration, as my notes of one experiment given above show, may not be reached for several minutes. This holds also for the Chelonians.

6. After stand-still, when the rhythm is resumed, the sinus is the first to beat, and may be followed by the auricles and ventricles, or by the ventricles only at first, *i.e.*, the auricles are often the last to recover, as in the Chelonians.

The results of stimulation of the vagus in the Alligator may be thus generalised :—

Stimulation of the vagus weakens the heart's action, and may cause an arrest of the auricles alone, or of the auricles followed by a brief stop of the ventricles; with a sufficiently strong current the entire heart is arrested, and remains so during stimulation, with marked increase in the usual diastolic relaxation; after a variable period of latency, the length depending on the condition of nutrition of the heart at the time, the beat is resumed; frequently the auricles are the last to begin; the beat of the heart is marked by acceleration, reaching a maximum in a variable time, and declining slowly or the reverse, according to the condition of the nutrition of the heart; the beat is also characterised by greater force, evident in both auricles and ventricles. The force and frequency are increased in inverse proportion to those prevailing at the time of stimulation.

It will be seen that the conduct of the heart in the Alligator under vagus-stimulation is very similar to that of the Chelonians, though in the hearts of the *Crocodylia*, with their two auricles and paired ventricles well-defined and separated,—in the shape of the latter especially, in the general character of the beat, &c.,—there is a considerable departure from this class. One looking at the heart of a small Alligator beating rapidly might believe, on superficial observation, that he had before him the heart of a mammal or bird; the colour of the blood issuing from wounds, especially about the head and upper parts of the Alligator, is much brighter than in the Chelonians, denoting a circulation admitting of better oxidation of the blood, and pointing to an advance in the animal scale.

III. Accessory Vagi.

From some previous experience with similar small nerves, in connection with the Sea-Turtle, to those I am about to describe, I was not wholly unprepared for a very remarkable result. These nerves may be traced in the Alligator from the glosso-pharyngeal, soon after its exit from the skull, down the neck, underneath the trachea, over the vessels, and to the heart. They were not more than a fifth or sixth of the thickness of the vagus in the specimens examined. They did not run close to the vagus but diverged from it, as they passed downwards more and more.

An extract from my notes of one experiment will give some idea of their function.

Experiment.—Nerve divided and peripheral end stimulated.

When the rhythm was 28, stimulation led to a fall to 20; when 12 to 6.

Force of beat is diminished; short stops, leading to an irregular rhythm.

On cessation of stimulation the rhythm rose from 28 to 35.

During the pause the normal diastolic relaxation was increased.

It is thus seen that in this case these nerves behaved exactly like the vagi; and, considering their origin and how closely related the vagus and glosso-pharyngeal nerves are anatomically, it seemed not unreasonable to suppose that some of the vagus fibres may have wandered off and taken a separate course to the heart.

This subject is further considered in my paper on the Sea-Turtle.

Whether they are always present, or have always the same action, I am unable to say without further examination.

IV. Accelerator Cardiac Nerves.

There passes from a ganglionic enlargement of the eleventh metamere towards the heart, and quite alone, a large well-defined nerve, as Gaskell and Gadow¹ have described.

I subjoin the results of two stimulations of this nerve in one case as illustrative of its influence.

¹ Vol. v. Nos. 4, 5, and 6 of the *Journal of Physiology*.

Experiment.—Heart beating with a regular rhythm of 29, a short stimulation of 11th metamere raises the rhythm to 32 from 29.

2. A second stimulation had the following effect :—

Rhythm during 1st minute of stimulation,	34
" " 2nd	32
" " 3rd	32

but it is to be noticed, that while during the second and third minutes the rhythm fell *the force of the beats increased*.

Thus it appears that the true test of an augmentor nerve is the amount of work the heart is enabled to do under its influence. I desire to call especial attention to this result, for it does not stand alone, and to a certain extent applies to the action of the vagus also.

Not only are cardiac accelerators augmentors and should be so called, but they increase the work done by the heart; for when there is a fall in rhythm it is so slight as to be much over-balanced by the greater force of the beat. Indeed, so far as my observation goes, this increase of the force of the beat is by far the most important matter. It is easy to see how one, on superficial examination of either an accelerator or the vagus, might be led into erroneous conclusions, especially if the *rate* of beat were alone considered.

V. Relative Power over the Heart of the Vagi, and the Results of their prolonged alternate Stimulation.

So far as I can judge from a very limited number of experiments, the right vagus, as in the Chelonians, has somewhat greater influence over the heart than the left; but both are usually very efficient.

I have also found that the heart is capable of prolonged inhibition by alternate stimulation of the vagi; but in the Alligator the nerves seem to die more rapidly than in the Chelonians, and it is doubtful if as prolonged inhibition could be maintained as in the latter; so far as my limited experience in this matter goes this is not the case.

VI. Peculiar Cardiac Inhibition followed by Acceleration.

In this connection I wish to discuss some peculiarities of reflex (?) inhibition, and describe an experiment which appears to be unique in physiology.

Experiment.—Small Alligator, about $1\frac{1}{2}$ feet long.

Medulla oblongata destroyed completely for more than one hour; both vagi divided; the latter dead throughout the greater part of their course.

Sharp tapping over stomach and liver, with an ordinary dissecting forceps, causes slowing, weakening, and brief stops of the heart. This lasts for about one minute after cessation of the stimulation, and is followed soon by a greatly accelerated rhythm (from 40 to 50). This rhythm is at first quite regular, but gradually diminishes and falls into irregularity.

This experiment is repeated three or four times with precisely similar results.

The only experiment known to me at all comparable with this is that mentioned by Marshall Hall,¹ and discussed by M^cWilliam on p. 239, Nos. 4 and 5, vol. vi., of the *Journal of Physiology*.

The last-mentioned writer would explain Hall's result as due to mechanical stimulation of the vagi nerves, by the jar caused by a blow to the stomach with a hammer in Hall's experiment, the brain and cord being destroyed. But in my experiment the vagi nerves were already dead throughout most of their length, and the jar of a blow from a pair of forceps cannot be considered as very great. On the other hand, the fact that the first effect was followed by regularity and acceleration of rhythm, certainly points to the vagus nerve.

I wish now to call attention to several phenomena which seem to me to demand careful consideration.

1. I have found in the fish that stimulation of certain parts, notably of the anus and tail, led frequently, and with moderate currents, generally to acceleration, either followed by slowing or not.

2. A similar result has been observed on stimulating the liver in the Sea-Turtle. In both the cases referred to the medulla and cord and vagi were intact.

3. On p. 271 of my paper on the Terrapin's heart,² reference is made to irregularity of rhythm as the result of stimulation of the main sympathetic stem, and I have observed on several occasions, what is not therein much insisted upon, that on first applying the electrodes to the part of the sympathetic therein

¹ Todd's *Cyclopædia of Anat. and Phys.*, art. "Heart."

² *Journal of Physiology*, vol. vi. Nos. 4 and 5.

defined, a brief slowing or stop of the heart has preceded the usual acceleration and augmentation of the beat.

McWilliam states that stimulation of the abdominal sympathetic does not lead in the Eel to cardiac arrest, and maintains that the afferent impulses are transmitted through the spinal cord to the medullary centre, when cardiac inhibition takes place after stimulation of the tail of the Eel.

But how upon McWilliam's hypothesis is my result of *acceleration* under such circumstances to be explained ?

There is one fact brought out in my experiments on the fish's heart with atropin which favours McWilliam's view.

After the free application of this poison to the heart of the fish I have not found it possible to get reflex cardiac inhibition as usual ; that is to say, we may get from this an argument that the vagi nerves, and these only, are concerned ; but again, if we assume that all the inhibitory fibres for the heart do not run in the vagus, necessarily this experiment does not carry with it so much force.

It is true that hitherto it has been believed that inhibitory fibres were confined to the vagus ; but in this paper I have shown that in the Alligator this does not seem to be so, and the case for the Sea-Turtle also favours such a view, as also perhaps what is referred to under (3) above.

As mentioned on p. 254 of my paper on the Terrapin, stimulation of the main sympathetic stem does in that animal produce the most decided cardiac inhibition, *and that when stimulation of the brachial plexus is ineffective*. Why is this, if the course of the impulses is along the cord ?

McWilliam explains the after-acceleration of reflex cardiac inhibition (stimulation of the vagus itself not being followed by such), by assuming in the Eel a "constant controlling vagal influence," which is weakened in the former case during stimulation. As a result of my eighteen experiments on this subject on the Slider Terrapin (see pp. 252 and 253 of the paper on that animal) no very strong case is made out for this view as regards this one cold-blooded animal.

It seems to me, when considering all these facts, that we should begin to seek for explanations more satisfactory than some of those now prevalent ; at present I have no view to

present that is free from difficulties; but many of the phenomena I have cited in this paper, and treated elsewhere, seem to point in the direction of possible cardiac inhibition other than through the main vagus stem, or possibly even its ultimate branches, though the latter have, apart from the main stem, been but little considered, in short, that some such view as that suggested by me on p. 271 of my paper on the Terrapiu may be rendered tenable by accumulating facts; but my object in this discussion of a very obscure subject has been rather to emphasize *facts*, and point out difficulties in the way of the complete acceptance of prevailing theories, than to offer new explanations.

If we assume that in the case of the fish and Sea-Turtle, as referred to in 1 and 2 above, the impulses pass along the sympathetic chain and then get into some cardiac accelerating branch, or even first pass along the spinal cord but not to the medulla, it is possible to understand the acceleration that first ensues under the circumstances referred to, without introducing the vagus at all.

In the case of Marshall Hall's experiment on the Eel, and my own on the Alligator, we may suppose the impulse to travel primarily along some inhibitory fibres not in the vagus stem, or not in the usual cardiac branches of that stem, and that these are finally overpowered by the influence of accelerating fibres. I found no more difficulty in this connection with M^cWilliam's objection that stimulation of the *abdominal* sympathetic in the Eel does not produce cardiac arrest than that stimulation of the same part in the Chelonians does not produce cardiac acceleration for stimulation of another part of the main sympathetic does. Impulses may have and do have a great variety of choice in the tracts they follow.

VII. *Stimulation of the Heart with the rapidly interrupted Current.*

The results depend in part on the strength of the current and in part on the condition of the heart at the moment of stimulation.

1. When the heart is fresh and in good condition the sinus can be arrested with as great ease as in the Chelonians, but when the heart is much exhausted, and the animal has been long

under experiment, arrest by any strength of current is quite impossible.

2. Stimulation of the auricles with a weak current causes dilation around the point of contact of the electrodes, and a weakening of the *rhythm* beat of the auricle. A stronger current wholly arrests the auricle, and the local dilation spreads over a wider area, finally embracing almost the whole auricle.

3. A moderate or strong current applied to the ventricles, when the heart is in good condition, causes a rapid intervermiform movement, followed by frequent stops. On the cessation of stimulation a long pause in the rhythm follows.

In all cases, no matter what part of the heart is stimulated, at the exact points at which the electrodes are applied, very small light-coloured areas may be seen, as in the case of fishes and Chelonians; also the usual blue appearance in the parts locally dilated, but I have observed in the Alligator an effect which is not to be seen in the fish or in the Chelonian heart. On the application of a very strong current to the edge of the auricles they are seen to exchange their natural bluish colour for a pallor—almost a whiteness; by carrying the electrodes along, more and more of the auricle takes on this appearance. The portion affected in this manner is thrown out of action. This, it seems to me, is the reverse of dilation, is, in fact, due, as also the finer smaller light-coloured points seen at the exact points of application of the electrodes when a weaker current is used, to a very marked and probably tetanic contraction of the heart-muscle. The dilation (local paralysis) may possibly be due, at least in part, to nerve influence, while the other is the result of the direct effects of the current on the heart-muscle itself.

THE FUNCTIONS OF THE TONSILS. By R. HINGSTON
Fox, M.D., M.R.C.P.

It is remarkable that, easy of inspection as the tonsils are, and frequently as they are affected in a large number of diseases, so little is certainly known as to their function.

The tonsils are the largest and most conspicuous portions of a ring of lymphatic structures, which extends around the pharynx and fauces. Thus there are very abundant nodules of adenoid tissue on the back of the tongue at its root, and numerous similar nodules on the sides of the pharynx about the orifices of the Eustachian tubes, whilst others are disposed on the hinder wall of the pharynx so as to form a band across it at this level.¹

The tonsil itself has been described as the largest mass of adenoid tissue in the body, being an aggregation of round nodules, composed of this tissue, and often, though not very appropriately, spoken of as "follicles." It is unnecessary to describe adenoid or lymphatic tissue in detail, further than to say that it consists almost entirely of small amoeboid cells similar to those of the blood, but many of them presenting double or partially divided nuclei, these cells being enclosed in a retiform matrix. There is an abundant supply of blood-vessels and of lymphatic plexuses, and the free surface of the gland is covered by a thick layer of stratified squamous epithelium. This surface presents many involutions, forming blind depressions, the crypts of the tonsil, into which the ducts of small mucous glands open, and around which the adenoid nodules are disposed. Such crypts are found also on the back of the tongue.

There is one further fact which may be here alluded to. It is stated by embryologists² that the fauces is the seat of what may be termed a developmental junction; that at this spot the inflected layer of epiblast which forms the lining membrane of the mouth meets the layer of hypoblast, which forms the major part of the alimentary canal. I lay no special stress upon this statement, but if it is well grounded it is of some interest. It has long been pointed out that new growths are apt to arise at such

¹ Kölliker, quoted in Quain's *Anatomy*, section *Pharynx*.

² Quain's *Anatomy*, 9th ed., vol. ii. pp. 878, 883, 884.

junctions, where tissues of differing affinities met. Now, it is curious that the fauces, if it be such a junction, should be the spot selected by so many diseases for the production of inflammatory lesions.

Passing on to inquire into the function of the tonsil, we may ask first, Does this gland belong to the respiratory or to the digestive tract? Unquestionably, to the digestive tract.¹ When the position of the gland is considered, and its relation to the surrounding structures during the acts of respiration and deglutition, no other conclusion can I think be arrived at.

Let us take the condition when the mouth is at rest and closed. The cavity of the mouth is then nearly obliterated; some space is left between the tongue and hard palate, but further back the velum palati (or, at least, its lower edge) lies in apposition to the tongue surface. If the fauces be attentively examined whilst the mouth is closing, it will be seen that the relaxed soft palate tends to assume a very sloping direction downwards and backwards, perhaps nearer to the horizontal than to the vertical, and that the pillars on either side arch outwards, also in a direction tending towards the horizontal.

Now the posterior arch of the soft palate is at a lower level than the anterior, and the hinder pillars are nearer together than those in front. This gives to the faucial arch a hollowed appearance in front, and this hollow is, in my belief, filled, when the mouth is closed, by the root of the tongue, which is convex from side to side as well as from above down. If this be so, the hinder pillars of the fauces lie against the tongue surface, as do those in front, and the tonsils, being situated on each side in the interval between the pillars, lie also against the tongue, and are shut off from the pharynx.

In support of these statements, I may allude to the moulded shape which the tonsil often assumes when it is enlarged and soft: thus, I have more than once observed the areæ distinctly mapped out upon its surface,—that facet which lay in contact with the tongue, separated by a ridge-like line from the facet which was in contact with the swollen uvula. It is also common, when a patient opens his mouth for inspection of the throat, to see vanishing strings or sheets of mucus, stretch-

¹ Cf. Dr H. Ashby in *Practitioner*, vol. xxxi. pp. 407 sqq.

ing between the pillars of the fauces or the tonsils, and the tongue surface with which they have just been in contact.

It will not be contested that normal respiration, after the period of infancy, takes place through the nose, the mouth being kept shut. From the posterior nares the respiratory tract will then pass down the hinder surface of the velum, and over the root of the tongue against which it lies, without entering the mouth, or coming in contact with the tonsils.

In the act of deglutition, on the other hand, each morsel of food, being grasped first by the anterior and then by the posterior lamina of the faucial arch, must necessarily be brought into contact with the tonsils,—indeed, it must actually be rubbed against their surface during its passage through the fauces. Surely the function of these glands, whatever it may be, must have some relation to that which is swallowed.

If further argument be needed to sustain the position that the tonsils belong to the digestive tract, it may be pointed out that, whilst there is no other considerable collection of adenoid tissue in any part of the respiratory tract, there exist in the lower part of the digestive canal bodies almost identical in structure with the tonsils, and connected with them by a close pathological relationship—the solitary and agminated glands of the intestine. It would be out of place to enlarge here upon this relationship, but it is a matter of great interest.

Besides, then, the presence of adenoid tissue in fine layers in the coats of the digestive tube, in the substance of the villi, &c., as indeed it is found in all the important tracts and organs of the body, there are these large and obvious collections of adenoid tissue in the wall of the canal—the tonsils and neighbouring nodules at the fauces, and the solitary and agminated glands in the intestines. As a class, these organs have been termed the “follicular lymphatic glands,” to distinguish them from the “conglobate” or ordinary lymphatic glands of the body.¹

The follicular lymph glands are separated only by the ordinary epithelial lining from the contents of the digestive canal. It is

¹ It need hardly be said that these latter differ only in their more complicated structure, being traversed by lymph channels, so adapted that the fluid may be brought into intimate contact with the adenoid nodules in its passage through the glands.

hardly possible to escape the conclusion that an interchange of some kind must take place between the glands and the food materials. What is the nature of this interchange? Their structure forbids the idea that these organs are secreting glands in the ordinary sense. They consist of closed nodules, without ducts, and without any gland cells other than the small white amœboid corpuscles alluded to.

Yet the writer of the article "Tonsil," in Quain's *Dictionary of Medicine*,¹ states, without any question, that the office of that organ is to secrete a lubricating fluid to moisten the fauces and aid in deglutition! This view appears to me wholly untenable.

As regards the solitary and agminated glands, we are not, however, left in any doubt. The process of absorption of fat particles in large quantity by the amœboid cells of these glands has been repeatedly observed by Schäfer² and others. That the glands are absorbent in function is what we should infer from their structure.

I am not aware that any observations of this kind have been as yet made upon the tonsil, except that Stohr has observed leucocytes passing apparently between the epithelial cells, and reaching the mouth.³ But in view of its structure, and of the ascertained function of the closely allied glands in the intestinal canal, it appears to me that we may safely conclude that the office of the tonsil also is one of absorption.

It will be objected to this view that the epithelial layer covering the gland is so thick as to render absorption through it improbable. The observation of Stohr just quoted would, if quite reliable, meet this objection, the more so as it has recently been shown⁴ that the absorbent processes which take place in the digestive canal are largely carried on through the agency of leucocytes. There is no *primâ facie* reason why white cells or their pseudopodia should not pass between the cells of a fairly

¹ Page 1647.

² *International Journal of Anatomy and Histology*, vol. ii. No. 1, 1885, pp. 6-29. I am indebted to Mr J. McCarthy, Lecturer on Physiology at the London Hospital College, for a reference to this paper. See also review of Zawarykin's researches, in *Lancet*, 1888, ii. p. 64.

³ Stohr, in Virchow's *Archiv*, quoted by Schäfer (*loc. cit.*), and by Landois.

⁴ Schäfer, *loc. cit.* Philipson states that absorption on epithelial surfaces takes place through the intercellular cement substance (*Lancet*, 1884, ii. p. 309).

thick layer of stratified epithelium in the moist living condition. Pathological considerations lend a further support to this view, for there is strong reason to believe that the tonsils absorb morbid poisons directly from the saliva.

It is not indeed likely that any considerable absorption can take place from the bolus of food as it passes rapidly through the isthmus of the fauces, encased in its glutinous covering of salivary fluid. But the fauces give passage to something besides food. I allude to the *Saliva*. During the intervals between meals,¹ a constant stream of this secretion is very slowly trickling through the fauces, converging from the floor of the mouth on each side, and from the dorsum of the tongue, to pass down over the root of that organ into the pharynx. In its passage the saliva not only fills the crypts and bathes the lymphatic nodules, with which this part of the tongue surface is richly furnished, but it must also, and especially, bathe the tonsils, since these organs lie in the groove on each side of the tongue and probably against its surface.

I believe the function of the tonsil to be connected with this stream of saliva, which is poured over it without cessation day and night.

It has been stated that the bulk of all the secretions which are furnished to the digestive canal, are reabsorbed by the blood-vessels of the segment below.² That this is so, for example, with some of the chief constituents of the bile, is generally believed.³ I ask then, Is it not reasonable to think that the tonsils reabsorb from the saliva, in the intervals of meals, certain of its constituents which would otherwise be wasted?

In conformity with modern views, we may regard the adenoid tissue of which the tonsils are composed as the birthplace of leucocytes. The materials which would be perhaps wasted in the stomach are thus, if my theory is correct, intercepted by

¹ That the saliva is secreted in considerable quantity when food is not being taken is evidenced in cases of salivary fistula, and by the dropping of saliva from the mouths of persons during sleep, which is often observed. The saliva is also, as we are all aware, not usually subjected to definite acts of deglutition, but passes imperceptibly through the fauces.

² See review of Brinton on "Food," in *Med. Chir. Review*, vol. xxx. p. 243. Dr Allchin in Quain's *Dict.*, p. 496.

³ See especially Tappeiner, reviewed in *Lond. Med. Record*, Oct. 1885, p. 423.

these glands, and made to minister to the growth of white cells.

The tonsils are apt to atrophy in middle and later life. Adenoid tissue everywhere is more largely developed in childhood, when not only nutrition but growth has to be provided for, than it is afterwards. And there is nothing surprising in the fact that these nurseries of young leucocytes (permit the fancy), planted here as it were by the river side, and drawing their sustenance from the nutrient stream, should dwindle in later life when the demand for white cells has become much less.

INVESTIGATIONS IN THE RELATION BETWEEN
CONVERGENCE AND ACCOMMODATION OF THE
EYES. By ERNEST E. MADDOX, M.B., C.M. Edin., *Syme*
Surgical Fellow in the University of Edinburgh.

(Continued from p. 508, vol. xx.)

V. *Distant Vision.*

WE have seen that with near vision the visual axis of an excluded eye generally deviates *outwards* from its fellow; it appears to be just as usual with distant vision for an excluded eye to deviate *inwards*. This is easily shown by pricking two pin-holes through a piece of paper at a distance of rather less than $2\frac{1}{2}$ inches from each other. On holding them horizontally before the eyes, and looking through the left aperture with the left eye at a distant object, the two circular images vary in their apparent relative position according to the distance of the paper from the eyes in such a way as to demonstrate the presence of relative convergence. More need not be said about this, since the camera acts upon the same principle.¹

Exp. 26.—The central and right lateral apertures² are used as in fig. 6, the stop being to the right.

The observer, instead of looking at the central aperture (x), as in testing for near vision, now looks through it at any very distant object, and while doing so moves the right slide till its aperture *appears* to lie just below the image of the central one.

If then the distance between the *actual* apertures be measured, they will be found separated by an interval rather *less* than the distance between the centres of the two eyes. Now, since the left eye is looking directly at the object, the image of the object, as well as that of the aperture which encircles it

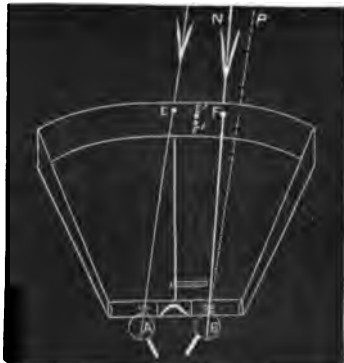


FIG. 6A. To illustrate the direct method with distant vision. (Erratum—x should be level with E', and y with F'.)

¹ A notice of this experiment was kindly communicated for me by Prof. Crum Brown to the *Proc. Roy. Soc. Edin.* in 1883–1884.

² At the time when the figure was made I used the right or higher lateral aperture. I now use the left or lower one to eliminate more completely the desire for fusion.

as in a frame, must fall on the left fovea centralis or point of acutest vision. The encircled image therefore is referred—where all foveal images are referred—to the line which bisects the angle of convergence. But the other aperture has been placed so that its image appears to be in the same line, or rather slightly below it; it therefore must fall exactly above the right fovea, on the median vertical meridian of the right retina. Since each image falls on a median vertical meridian, it follows that if the apertures themselves were separated by an interval equal to the intercentral distance, the visual axes would be parallel; if the interval were greater there would be relative divergence, but as it is, the interval is less, showing relative convergence.

Moreover, if, while the apertures are still kept in position, *both eyes* be made to observe distant objects through them, the images none the less appear superimposed; the amount of convergence attached to distant vision remains unaltered, whether one eye or both is used.¹ Since the natural outflow of energy from the converging centre when the desire for fusion is absent is a delicate comparative index of the accommodating energy, this fact shows that the activity of the accommodating centre is no greater when both eyes are used than when vision is confined to one, and corroborates the statement that accommodation is the work of a single innervation affecting both eyes equally at the same time. The object thus seen by the right eye, through the lower aperture, is one which really lies in a space to the *left* of the object seen by the left eye through the higher aperture. Thus,



FIGS. 7 and 8.—Objects (*a*, *b*) seen through the apertures of the camera.

if in figs. 7 and 8, *a* and *b* are two distant objects, *a* is seen by the right eye through the lower aperture, and *b* by the left eye through the higher one. Fig. 9 shows that for this to occur the visual axes must cross somewhere between the camera and the distant objects. This crossing point is at an average distance of about 112 inches from my own eyes.

Another glance at figs. 7 and 8 will make it evident that for the same object (*b*) to be visible by *both* eyes, the lower of the two apertures must be drawn away from its apparent position just under the other to the right. Let this be done till "*b*" is visible in both apertures, the *actual* distance between them will



Fig. 9.

¹ This presumes the possession of eyes of equal refraction.

then be the same as the distance between the centres of the two eyes, while the *apparent* distance between them will indicate the degree of relative convergence present. To measure it, we need only take the *difference* between the number of degrees now recorded and that previously recorded when the lower aperture appeared just under the other. In taking these observations on others it is essential, to obtain accurate results, that the arms should be supported; or better still, that the camera itself should be hinged (as mine is) on a stand, so that by telescopic action it can be raised or lowered to any required height, or inclined at any angle. It is difficult otherwise to maintain the requisite steadiness, and the arms get tired before the observation is complete.

The amount of Relative Convergence with negative accommodation.—This varies in different individuals, being apparently much greater in some than in others. In my own case fifty observations of the amount of relative convergence, associated with very distant vision, gave the average of $1^{\circ} 18' 43''$. By more than neutralising my half dioptre of manifest¹ hypermetropia I have never succeeded in reducing the convergence lower than $28' 30''$. For a hypermetrope such convergence excites no surprise; it would indeed be looked for, since the ciliary muscle, unlike that of an emmetrope, is never quite relaxed in distant vision, and a certain amount of attached converging effort might therefore well be expected to cling to it. But in fact the convergence noted is less in degree than with most of the emmetropic eyes I have tested. The unexpected feature is the comparative *smallness* of it, in the presence of hypermetropia. Were the connection between the two efforts as complete as it was once thought to be, as much as three and a half degrees of convergence would accompany each dioptre of hypermetropia.

Dr Bolton in six cases, without known hypermetropia, obtained an average inward deviation of $1^{\circ} 38'$, and I found that of a similar number of records to be $2^{\circ} 16' 14''$. The variations in these twelve persons were from 0° to 4° . Large relative convergence in distant vision appears to be generally associated with small relative convergence in near vision, and *vice versa*, though not without frequent and sometimes striking exceptions. In one instance slight *divergence* was found by Dr Bolton with negative accommodation, and in another, relative convergence

¹ "Manifest" hypermetropia is that which is discoverable without the use of atropine, while the remainder is latent.

noted for some time gave way, after a great nervous expenditure, to parallelism or even slight divergence of the visual axes, which continued for several days. I find that in the absence of exceptional causes of disturbance the amount of relative convergence attached to negative accommodation goes through a fairly uniform variation through each day, becoming greater as the day advances, but suffering a fall after each meal, though more especially after the principal midday one. The average A.M. record was $1^{\circ} 5' 12''$, and the P.M. record $1^{\circ} 24' 33''$, while the after-dinner one was $1^{\circ} 3' 4''$. The relative divergence in near vision (at 10 inches) diminishes through the day, though by far the greatest fall occurs during the first hour after rising. The convergence attached to negative accommodation and that attached to great positive accommodation do not, however, rise and fall together, for the relative divergence in the latter as noticed by the camera is *lessened* shortly after a meal, especially after the midday one, showing that the attached convergence is increased at the same time that that of negative accommodation is diminished. The average deviation, with vision for 10 inches, before the eyes were otherwise opened in the morning, was $7^{\circ} 36'$. In this I have not included an exceptional record of about $3^{\circ} 35'$ after disturbed sleep, consequent on the uncustomary taking of a supper on the previous night. It is known how irritation of the primæ viæ may cause temporary nervous strabismus in children; this record is so interesting, as showing how the same condition which causes a pathological effect at one age may at a later one cause only an unnoticed effect on the physiological condition of the centres, that I give here the observations of that day, and the one before and after it.¹

	7.15 A.M.	7.55 A.M.	8.20 A.M.	9 A.M.	10 A.M.
First day, . . .	$7^{\circ} 45'$	7°	6°
Second day, . . .	$3^{\circ} 35'$...	$4^{\circ} 15'$	$5^{\circ} 46'$	$6^{\circ} 26' 28''$
Third day, . . .	$8^{\circ} 20'$	$6^{\circ} 37''^*$

It may be noted that while the records of the first and third

¹ Owing to an imperfect marking of the camera these records are all slightly too large, though uniformly so; they serve for comparison only. The one marked * was earlier than the time given.

days *diminish* as usual, those of the second day gradually *increase* to the usual amount. Before attempting to estimate the effect of drugs and different conditions on the brain centres, it would be well for the observer to become acquainted with his own diurnal variations.

Point of Coincidence.—When an object is moved along that horizontal line of the sagittal plane which is level with the pupils, and looked at with one eye, there is a certain distance at which the meeting-place of the two visual axes coincides with the object. I name it the “point of coincidence,” since here the attached convergence coincides exactly with the accommodation to which it is attached. At this point there is neither relative convergence nor divergence; when the object is beyond it, there is the former; when within it, the latter. In some it might be rather a region than a point. Were the object moved along different radiate lines in the horizontal plane with direct oblique vision, the points so discovered would constitute a horizontal “line of coincidence,” and similarly a vertical line of coincidence could be found.

My own point of coincidence in the line first mentioned, which runs straight forward from the root of the nose, has varied from 56 inches to 14 inches distant. As might be expected from the fluctuations in the amount of deviation attached to near and distant vision, it shifts from minute to minute, according, doubtless, to the occupation of the eyes as well as the conditions of the nervous system.

The camera furnishes the most exact method of finding the distance of the point of coincidence, but the double prism is a much more ready means. With the former an object is approached till it is visible in the central and one of the lateral apertures at the same time that the apertures themselves appear superimposed; or, better still, a card coloured red to one side of a vertical line and green to the other, and provided with printed matter to insure exact accommodation, is carried on a traveller of a strip of wood hinged on to the stand of the camera. The left brass slide of the camera is withdrawn more than half its own length, so as to leave a short stationary *slit* instead of an aperture. With the stop to the left, place the card so that the median line on it is visible through the central aperture by the right eye; it is then made to approach or recede till the lines seen in the slit and the aperture appear continuous. This method permits of great nicety as well as speed. It is very important to insure that the eyes are accurately accommodated for the object. When this precaution is

taken, the variations are far less. Strangely enough, I have uniformly found the distance of the point of coincidence greater after very near vision of fine print, and less after distant vision. Another method I have employed is to use a long graduated strip of wood, at one end of which the double prism¹ can be fixed at pleasure; it rests on the mantelpiece or any convenient horizontal situation, and a night-light or other appropriate object is moved along it till the three images are exactly in a line. Objects should be avoided which have vertical edges if they are long enough to overlap. For self-trial a wooden traveller is used, which can be pulled backwards and forwards by a piece of string. This is the easiest expedient, but is not so exact or trustworthy as that with the camera.

When diplopia is heteronymous, it shows the point of coincidence is *beyond* the object, which must therefore be made to recede, and conversely to approach when diplopia is homonymous. It is easy to see the bearing of this point on the well-known clinical test, in which a flame at some distance serves for the object of view and a prism (base vertical) is held before one eye; of the two images which appear, one passes to the right or left of the other, according to the existing relationship between accommodation and convergence. The *distance* of the flame from the observer has been thought a point of little consequence, but the whole result depends upon it. If the distance is less than that of the point of coincidence, relative divergence will appear, while if greater, relative convergence will betray itself; provided, of course, that the prism is held absolutely vertical. If neither deviation is observed, the flame is exactly at the point in question; but if this happened with the flame at the usual distance of 7 or 8 feet, there would almost certainly be observed a wide deviation outwards if near vision were tested. Since the distance of the point of coincidence is generally less than that of the flame, slight relative convergence would be almost uniformly detected were the method sufficiently accurate, though the prismatic errors liable to occur in this test are far less than in those which require prisms of higher powers. The smaller the refracting angle of a prism, the smaller is the degree of accidental displacement of the image which attends any rotation of the prism from the vertical.

Seven cases examined by Dr Bolton showed an average of 43 inches for the distance of the point of coincidence. In one case it was 97 inches, about the usual distance of the flame in the clinical test spoken of, the result of which, therefore, in this case would have been negative, though with vision for 10 inches there was a deviation outwards of 7" recorded by the camera. Since the average distance of the point is less than that of the flame, relative convergence would generally show itself if the test were carried out with sufficient accuracy. There might be great outward deviation in near vision, or inward deviation in distant vision, or both, and yet neither be detected by the test as usually employed.

¹ The prism used is of a square outline, which gives no trouble in adjusting to the vertical, since one side rests on the wood.

The point of coincidence is of interest, because whenever vision of daily life wanders beyond it, the fusion effort, instead of acting through the converging apparatus, acts through some diverging mechanism, which is doubtless connected with the external recti, though it is just possible that it acts by inhibition of the converging centre. The nearer the point of coincidence is to the eyes the more fusion work falls through the day to the diverging mechanism and the less to the converging mechanism, and *vice versa*, so that its position is what determines the "division of labour" for these two innervations in their connection with the desire for single vision.

I may add that when an object is seen just within the "near point" with the double prism before one eye, relative divergence may for a moment disappear, or even give way to relative convergence, so great is the fruitless effort to accommodate more. The effort shows itself by the sympathetic effect on the converging centre—a good illustration of the fact that it is not accommodation and convergence that are united, but the nervous *efforts* in the ganglia of the 3rd nerve which cause them. For this experiment care must be taken to avoid obliquity of vision or to allow for its presence.

If two horizontal slits are cut in a piece of paper or cardboard, so that the inner end of each terminates in the vertical middle line of the card, and yet so that one is on a level about $\frac{1}{2}$ inch higher than the other, the point of coincidence can be found in a very simple and inexpensive way, without either prism or camera, by looking through the slits at any vertical linear object till it appears continuous in each. It is not very trustworthy, however, in a patient's hand, since obliquity may cause fallacy.¹

The Three Grades of Convergence—We may now distinguish the three elements of that complete convergence which occurs with binocular vision of a near object.

- 1.² *Initial Convergence*—which is that attached to negative accommodation.
2. *Accommodative Convergence*—which is that, in addition, attached to positive accommodation.
3. *The Fusion Supplement*—which is that excited by the desire for fusion to make up, when it can, for the deficit (or excess) of the other two.

¹ Two horizontal stenopaic slits at different levels, placed in the ordinary trial-frame, would act on the same principle.

² It is convenient to use contractions for these—I.C., A.C., and F.S. respectively; also, R.C. for relative convergence, R.D. for relative divergence, and P.C. for the point of coincidence.

Fig. 10 illustrates these three factors in looking at a point O. The first brings the visual axes from parallelism *pp* to *ii*, the second to *aa*, and the third to O. Were O at the point of

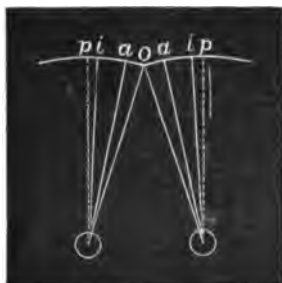


FIG. 10.—The three elements of convergence in near binocular vision of a point O.

coincidence it would coincide with *aa*, and the third factor would be engaged only in steadying the eyes by counteracting the tiny inequalities in the evolution of that nervous energy which maintains the other two. For objects beyond the point of coincidence there are only the first two factors in convergence in exercise, the fusion supplement being employed no longer in *augmenting* but in partly *neutralising* their effect.

The distinction between the initial and accommodative convergence is important, because they are unequally affected by different conditions. Thus we have seen that the effect of a meal is to diminish the former and increase the latter so much, that it more than makes up for the initial diminution. Initial convergence is affected directly by the sympathetic system through the external recti, while the accommodative convergence is only affected by changes in the cerebral centres of the 3rd nerve when vision is near, and the 3rd and 6th when vision is more remote. We have already seen how to measure the initial convergence and the relative divergence in near vision—the difference between the two gives the accommodative convergence.

Squints may be analysed into their initial and accommodative elements by careful measurement, first with negative accommodation, and then with positive, by the direct or blind spot method, as required.

The accommodative convergence can itself be analysed by finding how much of it belongs to each dioptré of accommodation. To do this objects are viewed at 1 m., $\frac{1}{2}$ m., $\frac{1}{3}$ m., and $\frac{1}{4}$ m. distance in turn; but an average of a great many experiments must be made to get results of any value. Dr Bolton's experiments¹ show that the convergence attached to the *first* dioptré is the greatest in his case, being $3^{\circ} 18' 27''$. To the 2nd D was

¹ Kindly made at request, February 1886.

attached only $45' 18''$; to the 3rd D— $2^\circ 54'$; and to the 4th D— $2^\circ 20'$. The excess of the first over the others fully accords with the fact that the point of greatest R.C. is not at practical infinity. Objects at the same distances give in my own case $1^\circ 53' 42''$ — $1^\circ 13' 37''$ — $1^\circ 41' 40''$ —and $2^\circ 44' 24''$ of accommodative convergence for these four dioptries respectively. The first is greater than the next two, the second is, as with Dr Bolton, the least, but the fourth is the greatest of all, owing doubtless to the greater effort needed for this dioptrie than for the previous ones, just as a man must put forth more effort in raising a weight through the fourth foot from the ground than through the first foot owing to increasing mechanical disadvantages. A dioptrie is a unit of work, not of effort, and since in a hypermetrope these four dioptries are not the *first* four, the effort required for each begins to increase more rapidly than in an emmetrope. No doubt each succeeding dioptrie, and each succeeding degree of convergence, needs more effort than the preceding one, but the resistance experienced by one effort may increase more rapidly than that experienced by the other, and the amount of convergence attached to each unit of accommodation varies accordingly—at least in near vision uncomplicated by any diverging effort. In testing the *true* initial convergence of a hypermetrope, the compensating lenses worn must have their optical centres separated by the exact intercentral distance of the observer, to avoid their prismatic fallacy—even then an error exists, proportionate to the strength of the lenses and the degree of initial convergence, for which a subsequent formula gives the correction. I prefer, to avoid this, to place a single lens of $9\frac{1}{2}$ inches greater focal length before the central aperture, or else before the slit made by largely withdrawing the left brass slide, the end of which can then be placed apparently under the central aperture.

The prismatic action of such a lens introduces no error at all. The farther a lens is from the eyes the more it relieves accommodation, because its focus is brought by so much the nearer to the retina; hence a weak lens at a distance has the same effect as a more proximate and stronger one. For this reason old people sometimes prefer to wear their spectacles on the tip of the nose.

Since spectacles are almost never worn nearer than half an

inch from the dioptric centre their power does not exactly express the relief they give to the accommodation—half an inch at least must be subtracted from their focal length to do this. Hypermetropia therefore is always slightly greater than the trial lenses indicate, and, conversely, myopia is always less. But this is a digression—it is to illustrate why a lens at the base of the camera must be weaker than one before the eyes. I have as yet by such lenses only been able to *reduce* my initial convergence, and have never obtained complete parallelism of the axes.

Point of greatest relative Convergence.—In glancing with one eye at objects intermediate between practical infinity and the point of coincidence I had thought that the amount of relative convergence diminished uniformly with each approach of the point of view, until at the point of coincidence it gave way to commencing relative divergence. But Dr J. S. Bolton discovered that in his own case the relative convergence at first *increased* as vision became less remote, reaching its maximum when an object is viewed at 5 metres; within which it gradually diminished up to the point of coincidence. His “initial convergence” was $1^{\circ} 10'$; relative convergence *increased*, with accommodation for 8 metres, to $1^{\circ} 44'$; for 6 m. to 2° ; and for 5 m. to $2^{\circ} 12' 36''$. It was here therefore nearly twice as great as the initial convergence. At 4 m. it fell again to 2° ; at 2 m. to $1^{\circ} 42'$, so it was still greater than the initial convergence; at 1 m. to 1° ; then came the point of coincidence at the distance of .85 m. (34 in.).

At half a metre (20 in.) there was relative *divergence* of $1^{\circ} 24'$; and at the distance of the apertures of the camera (.25 m.) the divergence reached 6° . On testing another subject he found “the point of greatest relative convergence” to be 6 m. from the eyes. In this case the increase was not so marked, the “initial” convergence being $1^{\circ} 5' 24''$, while at 6 m. the record gives only $1^{\circ} 45' 36''$. At 2 m. the relative convergence was still greater than the initial, being $1^{\circ} 18'$. The point of coincidence was at 1 m.; and the relative divergence, though being $2^{\circ} 15' 36''$ at half a metre, was at the distance of the camera 6° . In these two cases the conditions with vision for 10 inches were therefore the same, but the smaller initial convergence in the latter seemed to throw the two points of “coincidence” and of “maximum relative convergence” to a slightly greater distance.

The results in my own case vary too much to be of any value in regard to this phenomenon, the relative convergence at 8 m. being sometimes more and sometimes less than the initial convergence; but since the refraction is abnormal, this is no guide to the physiological conditions.

To summarise: If we look at accommodation and the convergence attached to it as two racers beginning from infinity, convergence has the first start, and gains still more up to the point mentioned by Dr Bolton; it then slowly falls behind, till at the point of coincidence the two are abreast; it then continues to fall behind, and thus creates the relative divergence of near vision; but just at the near point—the end of the race—it again gains ground, and comes in abreast or even in front of accommodation.

The Point of Repose.—It has been known for some time that the visual axes are not parallel when the eyes are completely at rest, *i.e.*, without being engaged in the vision of any special object, or affected by any act of volition;¹ but it is difficult to determine at what point the axes meet. It is not the point of initial convergence, for that is attached to negative accommodation. And it is well known that the ciliary muscle can by very few, if by any, be completely relaxed without the aid of a distant object to excite the desire for distinct vision; so that in a state of rest there is some positive accommodation, which cannot exist without being accompanied by a due proportion of attached convergence of the visual axes in addition to the initial convergence.

The natural position of eyes in the dark I have tried to determine by the following experiment.

Exp. 27.—Use the central and left lateral apertures of the camera, with the stop to the left; but in looking into it cover the apertures outside with a black pad, so as to produce the impression that the eyes are looking into absolute darkness. A momentary displacement of the pad (a penwiper does well) reveals the two apertures and covers them again before there is any attempt to accommodate for them. The left slide can be moved by repeated trials till, on moving the pad, the images appear in the same vertical line. The real distance between them then, of course, records the separation of the visual lines at the distance of the base of the camera. The records vary in my own case from 5° to 8° 30',¹ being generally only slightly

¹ Mr Brudenell Carter has expressed his belief that "in states of rest the internal recti possess the physiological preponderance over the externi which

different from the disposition of the axes when one eye is occupied in vision at 10 inches. This is somewhat unaccountable, since the radiate appearance of the apertures shows that accommodation does not occur for them.¹ The average of observations taken on nine different occasions was $6^{\circ} 26' 16''$, while that of the relative divergence at 10 inches on the same occasions was $6^{\circ} 49' 36''$, so that the visual axes would meet at the distances of $18\frac{1}{2}$ and $19\frac{1}{2}$ inches from the eyes respectively. Many of the observations were taken in the morning before the eyes were otherwise opened; but though the point was at that time rather more remote, the difference was not greater than that of the natural relative divergence in near vision at the same period. It is difficult to believe that so near a point of meeting of the visual axes should be the real position of rest. It may be that a psychical effect is produced by looking into blank darkness, since near objects are the ones that would be instinctively looked for in such a state. Still, on closing the eyes and then opening them suddenly, the apparent position of the apertures only confirms the results. When the light was so reduced that the mind could only detect the dimmest indications of apertures, they appeared together when really separated by 10° , so that the visual axes did not meet until nearly 34 inches from the eyes. On looking at a dull surface without attempt to accommodate, the results were intermediate between those of the last two methods ($8^{\circ} 15'$). The position taken by the eyes of a patient under chloroform is not a very trustworthy indication of the position of rest; the effect on the pupils points to probable disturbance of other ocular centres. That the external rectus is partly supplied by the sympathetic is an interesting fact, as showing to that extent an antagonism between the sympathetic and the 3rd nerve in the ocular movements we are now considering, analogous to their antagonism in the movements of the pupil; chloroform would be likely to affect them in a similar way. In one case I noticed marked external strabismus under chloroform, which continued no longer than the anæsthesia.² The eyes made constant tiny oscillations from side to side, and the margin of the cornea was $\frac{1}{4}$ inch above that of the lower lid. The pupil at first widely dilated, but shortly after the disappearance of the conjunctival reflex it began

flexor muscles commonly possess over extensors, and the eyes during sleep or anæsthesia are just a little convergent, in the same way as the limbs are slightly flexed." "This preponderance," he says, "is probably increased by the fact that in the conditions of civilised life the externi are less used than the interni

¹ For these experiments, as indeed for all, a piece of black silk depends from the lower margin of each wooden slide at the narrow end of the camera, to exclude vision of other objects.

² To give full attention to the respiration, and yet have one hand free for the eyes, it is useful in administering chloroform to women to hold the left end of the towel between the thumb and the forefinger of the left hand, so that the tips of the middle and ring fingers rest continuously against the clavicle, and appreciate the former the rolling movement of its anterior surface against the side of the last phalanx, and the latter its upward movement against the tip. The right hand is then free, when not adjusting the towel, to open both eyelids by its first and little fingers.

gradually to contract, taking a long time to get to the size of a pin's head. On the removal of the chloroform it remained thus for some time, then suddenly dilated nearly to its full, this preceding the return of the conjunctival reflex. On reapplying the chloroform it slowly began to contract again, taking as before a long time to reach its minimum size. This was its uniform behaviour during the two hours' administration for an intra-peritoneal operation. The strabismus may have been reflex from the abdomen.

The intercentral distance.—There are many methods of finding the distance between the centres of motion of the two eyes. (a) The simplest and best is to look at a linear vertical object at a great distance through the camera, moving one of the slides till the object appears to bisect the central and one of the lateral apertures, as attention is directed to each in turn. The distance between the apertures gives the intercentral distance;¹ while the number of *degrees* recorded between them expresses the exact magnitude of the "optic angle" (*i.e.*, the angle included between the visual axes) of the person tested when he looks with both eyes at the central aperture; since it is through the "alternate" angle that the one visual axis must rotate out from that point in order to become parallel with the other (Euclid, I. 29). This angular record is the one most convenient to preserve, since to obtain the "initial convergence" at any time it is only necessary to deduct from it the record given when the simple observation is taken of looking at a distant object through one aperture and placing the other apparently beneath it. To convert the angular dimensions into linear ones, it suffices to know the linear equivalent of each degree. It is .1789 inch, with vision for 10 inches. From this a table may be made.

Table of the Linear Value of Degrees at the Base of the Camera.

	Inches.	mm.		Inches.	mm.		Inches.	mm.
12°	2·1468	54·468	13° 30'	2·4151	61·276	14° 50'	2·6537	67·329
12° 10'	2·1766	55·224	13° 40'	2·4450	62·033	15°	2·6835	68·085
12° 20'	2·2064	55·981	14°	2·4748	62·789	15° 10'	2·7133	68·841
12° 30'	2·2362	56·737	14°	2·5046	63·546	15° 20'	2·7431	69·598
12° 40'	2·2661	57·494	14° 10'	2·5344	64·303	15° 30'	2·7729	70·353
12° 50'	2·2959	58·25	14° 20'	2·5642	65·059	15° 40'	2·8027	71·11
13°	2·3257	59·007	14° 30'	2·5940	65·816	15° 50'	2·8326	71·867
13° 10'	2·3555	59·763	14° 40'	2·6239	66·572	16°	2·8624	72·623
13° 20'	2·3853	60·52						

¹ The measurement being partly on a curve, there is a slight error of .004 inch. It may be avoided where great accuracy is required by using the left aperture 7° away from the middle line instead of the central one.

From this table, if either the intercentral distance or the optic angle in binocular vision for 10 inches be known, the other may be found. The radius is 10.25 inches, since the centre of motion is behind the optical centre.

(b) It is not always easy to find a suitable linear object at sufficient distance. If the camera is mounted on a stand it can, after adjusting the central aperture for any distant object, receive a slight tilt to bring the other aperture to the same level. The tilt would always be through the same angle, and can with my own stand be mechanically provided for when this method is employed.

(c) In *practice*, however, the object is far more convenient within the room. To open a window is not advisable always, and to look through it may introduce some prismatic error from the panes. Any linear object may be viewed—if at 17 ft. 1 inch from the *base* of the camera the distance between the apertures must be increased by $\frac{1}{20}$ th, if at half that distance by $\frac{1}{10}$ th. I now use a card marked with a vertical strip of white, $\frac{1}{4}$ inch wide, down the middle, to the right of which is all coloured red, and to the left green. After adjusting the camera so that the white strip is visible in the central aperture with an equal band of colour on each side, it is easy to know whether to push the lateral aperture in or out by whether the red or green colour is that seen through it. This expedient greatly compensates for want of intelligence in the patient. The one source of fallacy in all methods with a near object springs from the varying distance in different patients between the corneæ and the apparatus; but the greater the distance of the object the less the error. The card can either be connected to the base of the camera by a string of the required length, or it can be placed on the strip of wood already mentioned at the distance of 41 inches from the eyes; the latter is now my usual practice, being much the handiest and quickest indoor method. The record must be increased by adding a third as much again. An object nearer than this is not advisable. In testing for the relative convergence or divergence, when accommodation is exerted for objects nearer than practical infinity, it is useful to know how many marked degrees at the base of the box would be intercepted between the visual axes, were they both directed accurately at the object viewed. To

find the amount of deviation it is then only necessary to deduct from this the degrees recorded when, in looking at the object through one aperture, the other is placed apparently beneath it. The separation of the visual lines at the distance of the base of the camera in binocular vision of any object is given by the formula $x = \frac{i \times d}{d - 10.25}$, where x is the required number of intercepted degrees, i is the intercentral distance, and d the distance in inches of the object from the eyes.

VI. *Direct Oblique Vision.*

So far we have considered the relation between convergence and accommodation apart from any influence which may be exerted upon either by one of those innervations which turns both eyes to the right or left. Whenever the point at which the visual axes meet lies to one or other side of the median plane, a new innervation comes into play. Does the intervention of this new effort in any way disturb or alter the relationship we have been considering? We can only judge of efforts by their results, and these results are in oblique vision complicated by the fact that accommodation and convergence are required in differing proportions when an object is viewed with different degrees of obliquity. This, indeed, is in itself ample reason why the two are not so inflexibly bound together as they were once thought to be, and as the two accommodating mechanisms actually are. Complete central connection might at first sight appear the simplest conception. But in daily life the eyes need constantly to wander from side to side, and as they do so, accommodation and convergence are required in as constantly differing proportions, which make a certain "play" between the two innervations a necessity, and for which provision is made by superadded functions which can reflexly increase or diminish either as required. But might not these have been done without, by such an adaptation of the central connections that each ranging effort would in a direct way produce the required modification in the others? No, for up to a certain geometrical degree of obliquity accommodation needs to be relatively increased, while beyond it convergence needs to be

increased. Why, then, if to attain this play central connection must in part be overcome, is there any such connection at all? It is a great saving of the reflex fusion-effort.

It is evident that geometrical considerations must precede the physiological study of the subject of oblique vision.

(a) *Accommodation*.—Apart from any connection with convergence, disproportion between the accommodative requirements of the two eyes is brought about by the slightest deviation of

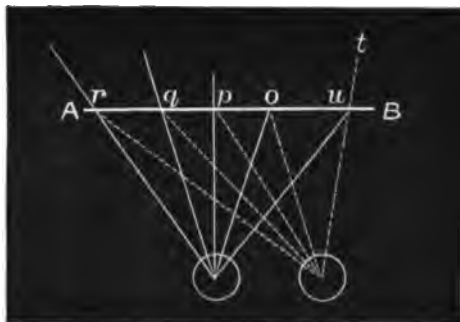


Fig. 11.

the point of fixation from the median plane. Fig. 11 illustrates this when any flat object is looked at, as in reading a book. The prolongations of the visual lines on the distal side of the line AB represent the disproportion.

Thus, when both eyes are looking at "u," the object is nearer to the right eye than to the left by the distance tu , and so on. Every departure of the point of fixation from the middle line lessens the required accommodation in the opposite eye, while at first it increases that of the eye of the same side till the fixation point has traversed a distance op equal to half the intercentral distance, after which it falls through a similar interval pq to the original amount, and then continuously diminishes. But the centres for accommodation are so intimately connected that one eye cannot accommodate more than the other. When variations, therefore, exist either in the refractive power or requirements of the two eyes, "that eye has the bright image which attains it most easily at the expense of the other" (Donders). They do not split the difference; if they did so there would be diffusion circles in each eye. Since accommodation with normal refraction implies positive effort, that eye which is *farthest* from the object, and can see it with least effort, determines the accommodation for *both*. Fig. 12 therefore represents "the line of equal accommodation" for near vision, in whatever point of which the

object is placed accommodation remains the same. It is composed of two arcs of equal radius, described from the centres of their opposite eyes.

In hypermetropia the line is similar; the reasons for it being so are intensified, since accommodation is a greater effort; but in myopia accom-



Fig. 12.

Fig. 13.

modation is negative outside the line which limits the far point, and which is made by drawing each arc from the centre of the eye of the *same side*. Since in these cases relaxation is often attended with more effort than accommodation (owing to spasm of the ciliary muscle), the "line of equal convergence" would be of the same shape as the "far point line" for some distance within it.¹

(b) *Convergence*.—Fig. 11 shows that convergence, as well as accommodation, diminishes with oblique vision; but that they do not diminish equally is made clear by the fact that the line of equal convergence (fig. 12) is not of the same shape as that of equal accommodation (fig. 13).² The former is part of a circle which passes through the centres of motion of the two eyes (not like the horopter through the dioptric centre), and possesses these properties. (1) The angle of convergence is the same whatever point in it is made the point of binocular fixation. (2) In glancing from any one point in it to any other, both visual axes traverse equal angles; thus in fig. 14 the angles $O B c$ and $O A c$ are equal; while, in contrast to this, fig. 11 shows that in glancing from O to q or O to p , the left axis passes through a greater angle than the right; as it does, indeed, whatever point is looked at to the left in the straight line AB . (3) The line

¹ While what has been said holds good in normal vision, since attention is seldom directed to one side for long at a time, a fallacy must be guarded against in experiments which require *sustained* obliquity of the visual axes; the visual apparatus of the farthest eye might weary, and for a time permit the accommodation of both eyes to be governed by that of the nearest one, and thus be increased.

² These were called in the original thesis the "Isostigmal" and "Isogonal" lines respectively, but I do not see the necessity of naming them.

which bisects the angle of convergence is the one to which hypothetically objects upon the maculae should be mentally

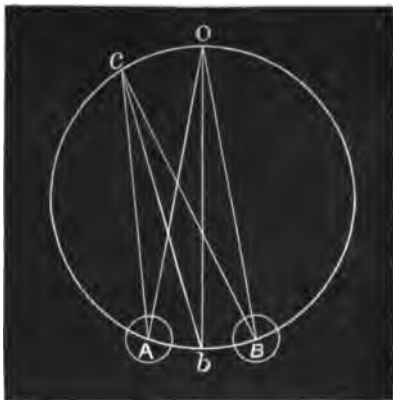


Fig. 14.

referred. Whether, in fact, they are so physiologically remains to be proved. The line is obtained by uniting the point of binocular fixation (*c*, in fig. 14) to the posterior point of the circle (*b*). The position of this posterior point shifts, of course, with every variation in the size of the circle; the line *cb* itself is inclined to the median plane by an angle which measures the

obliquity of vision, since it is equal to the angle which *each* visual axis has traversed in looking from the anterior point of the circle (*c*) to any other point in it (*c*). This angle, therefore, represents the "ranging" work to be done in looking at any such point. I do not say the ranging *effort*, for, as before mentioned, effort is often disproportionate to work, owing to greater resistance or other disadvantages. A certain evolution of nervous energy from the converging centre produces a definite angular deflection inwards of both visual axes, and similarly an effort of a ranging centre produces a definite deviation of both visual axes to the right or left. The nervous impulses perform angular work, if I may so say, as far as vision is concerned, and therefore we may assume that it is by angles that the mind judges of the work done in estimating the projection of the field of vision; but since the judgment is based solely upon the *effort* put forth, any discrepancy between effort and work would show itself in angular misjudgment, unless by habit the mind had come to associate a certain degree of effort with the work it *usually* performs, instead of with the work it *should* perform compared with a smaller effort. Such allowance is no doubt made, in whole or in part, except for unusual obliquities. Were "effort" and "work" exactly proportionate in both the converging and ranging innervations, all objects seen by the fovea of one eye or

given point (*c*) is to describe a circle through it and through the centre of each eye,¹ as in the figure, and from the centre of the farthest eye (*B*) to draw the arc *cx* from *c* to the median line. The circle is the line of equal convergence for that point, and the arc is part of the line of equal accommodation for the same. In binocular vision, therefore, of the point *c*, convergence must occur as if for *O*, and accommodation as if for *x*, while both eyes are deviated to the right through the equal angles *OBc*, *oAc*. The point *b* gives the base of the line which bisects the angle of convergence, and which is made by joining *bc*, while the inclination of this line to the median plane expresses the angular ranging movement of the two eyes. Were the relation between convergence and accommodation inflexibly complete for objects in the middle line, there would be diplopia for any object out of the middle line, except at one point on each side, within which diplopia would be heteronymous from relative divergence, and without which it would be homonymous from relative convergence. The nervous ties, therefore, though strong enough to relieve fusion-effort, are not so strong but what they can be overcome to meet such requirements.

The lines of equal convergence and accommodation, if rotated round the intercentral line as an axis, would describe *surfaces* of equal convergence and accommodation respectively.²

¹ This may be done by drawing from *A* and *B* straight lines at right angles to *cA*, *cB* respectively. From the point where they meet draw a straight line to *c*, the bisection of which gives the centre of the required circle. Or *Euclid*, iv. 5.

² (1) To find the line of equal convergence for any required angle of convergence—the *radius* of the required circle is found by dividing half the intercentral distance by the sine of the angle. (It may be found *geometrically* by *Euclid*, iii. 33.) (2) To find the angle of convergence when an object is viewed in the median plane at a given distance from the eyes—half the intercentral distance, divided by the distance of the object from the eyes, gives the sine of half the angle.

(To be continued.)

SIX SPECIMENS OF SPINA BIFIDA WITH BONY PROJECTIONS FROM THE BODIES OF THE VERTEBRÆ INTO THE VERTEBRAL CANAL. By Professor HUMPHRY, F.R.S. (PLATES XVII., XVIII.)

1. THE first specimen was taken from a child who died a few days after birth. The sac, which was very thin, and covered the sacral and lumbar regions, had burst, and a bony prominence was felt in its middle.

The vertebral canal is widely open below the 1st lumbar arch, the laminae of the four lower lumbar and the sacral vertebræ being all directed horizontally outwards. The arches of the 11th and 12th dorsal vertebræ are directed normally, but are incomplete, the vertebral canal being at this part widely open. The arch of the 1st lumbar vertebra is, however, completed by cartilage; and a curved bony process (or bar) ascends from, and has grown out of, the back of the body of the 2nd lumbar vertebra (rather, as the section, fig. 3, shows, from the intervertebral substance between the 1st and 2nd lumbar bodies), bisects the vertebral canal, and impinges upon the under edge of this cartilaginous arch. From the back of the bodies of the 3rd and 4th lumbar vertebræ rises a second much larger osseo-cartilaginous process, bridging over and uniting these two bodies, and rising considerably above the level of the dorsal and lumbar arches. It forms one mass at its base, but is partially bifid towards its summit. It slants forwards, and its base partially extends over the body of the second lumbar vertebra. The 1st and 2nd sacral vertebræ appear to be normal, with the exception of the lateral direction of their arches; but the vertebræ below these are irregular and confused and curved to the left; and the coccyx is represented only by a cartilaginous knob (fig. 3 b). The dorsal bodies and the arches, above the 11th, are normal, except that the spine is bent a little to the left, and the arches and transverse processes of the 9th, 10th, and 11th vertebræ, where the curve is most marked, are, on the left side, approximated and anchylosed, and the extremities of their transverse processes are covered and united by a thin band of cartilage (fig. 2, c).

A vertical section (fig. 3) from before backwards, in the median line, or in parts slightly to the right of it, shows the bodies of the vertebræ in regular serial order and in normal form. But the body of the 3rd lumbar vertebra is small, not being more than half its proper size, and that of the 4th is somewhat smaller than natural. Placed behind these, separated from them and from one another by cartilage resembling that between the bodies of the vertebræ, are two spheroidal spongy bony masses resembling vertebral bodies. That over the body of the 3rd lumbar vertebra, which appears stunted by it, is the larger. These form the base of the large projection into the spina bifida; and, connected with their posterior aspects by cartilage, are bony processes, somewhat denser, with foramina¹ between them, suggestive of rudimentary and misshapen vertebral arches, which form the summit of that projection. The cartilages intervening between the spongy bone-masses, and separating them from the vertebral bones in front of them, resemble the intervertebral cartilages, inasmuch as each is, like them, composed of two cartilage-plates appertaining to the adjacent bones with an intervening softer plate foreshadowing, apparently, an intervertebral disc. Indeed, the section of the projection is very suggestive of its being formed by two supplementary vertebræ developed behind the bodies of the 3rd and 4th lumbar bodies, and growing into the vertebral canal. The azygos bony process, situated further forward, is seen to extend from the cartilage between the 1st and 2nd lumbar vertebral bodies to the cartilaginous arch of the 1st lumbar vertebra, and to be continuous with both these cartilages.

The spinal cord and membranes passed down to the 1st lumbar vertebra, retaining the normal condition to this point, and presenting no bulging at the vacant space in the arches of the 11th and 12th dorsal vertebræ. Beneath the arch of the 1st lumbar vertebra it apparently divided, passing on the sides of the mesial bony bar, and then expanding upon the under surface of the back part of the sac, as is usual in cases of spina bifida.² It and the wall of the sac were quite free from the bony eminence,

¹ These foramina did not, so far as I could discover, contain or transmit any neural elements.

² See paper by me on spina bifida, this *Journal*, vol. xx. p. 500.

which was smooth and covered by the dura mater and the lining of the sac. The nerves leaving the cord traversed the sac; being separate and free in it, on their way to the lumbar and sacral intervertebral foramina. One or two of them, however, were applied upon the sides of the large bony process, and connected themselves with, or traversed, the membrane covering it.

The peculiarities in this specimen are—

First. The deficiencies in the vertebral arches above the spina bifida, and separated from it by the complete arch of the 1st lumbar vertebra, below which the spina bifida commenced, this deficiency not being attended by any abnormality in the cord or its membranes at this part. There was merely a deficiency in the growth of the arches, without that deficiency in the segmentation of the spinal cord and its coverings, which is usual, and is indeed a prime feature, in spina bifida.

Secondly. The bony processes projecting from the bodies of the vertebræ into the vertebral canal. Processes, similar to the upper one of the two in this specimen, passing from before backwards in the middle line, and bisecting the spinal cord, have occurred, and are mentioned in the Report of the Spina Bifida Committee (*Transactions of the Clinical Society*, vol. xviii.); but in this instance there was a second large osseo-cartilaginous growth projecting into the sac, covered by the anterior wall of the sac, and free from the posterior wall, and consisting apparently of the bodies and processes of two vertebræ placed behind two of the lumbar vertebræ, and connected with them and with each other in a manner similar to that which usually obtains between the vertebral bodies at the time of birth. Whether these two are to be regarded as displaced vertebræ, vertebræ shunted, as it were, behind the others, or as supernumerary vertebræ, is difficult to decide. Indeed, the morphological significance, if they have any, of these pseudo-vertebræ and the azygos bar in front of them, I must leave for the consideration of those who are better versed than I am in the vagaries of the developmental processes.

Thirdly. The deficiency in development of the lower part of the sacrum and of the coccyx, the curves in the spine, and the ankylosis of the vertebral arches, are worthy of note.

2. Professor Stewart, at the College of Surgeons in London, has been so good as further to dissect for me and make drawings (Plate XVIII.) of the interesting specimen (No. 276c) in that museum presented by Mr Jackson of Wolverhampton, and represented and partially described in the Report on Spina Bifida given in the *Transactions of the Clinical Society*, vol. xviii. This further dissection shows that the specimen really consists of $4\frac{1}{2}$ vertebræ, viz., the 11th and 12th dorsal and the 1st, 2nd, and half of the 3rd lumbar, and that the bodies of the 12th dorsal and 1st lumbar are fused together, forming what appears as one body. The evidence of the individuality of these two is furnished by their arches and processes being separate, with a separate intervertebral foramen on each side, which was of quite its natural size, and had a nerve passing through it. There is also a band of intervertebral substance surrounding the apparently single body, and dividing it into an upper and a lower portion; and a slight extension of this substance upwards and downwards indicates the line of division between the bodies and the pedicles of the arches. The horizontal bony process traversing the vertebral canal passes backwards from between the bodies of the 1st and 2nd lumbar vertebræ. It is broad at its base, where it appears to have encroached upon the bodies of the contiguous vertebræ, especially of that above it; and its irregularly quadrilateral extremity, which has a deep pit in its middle, occupies the ends between the laminae of these vertebræ (the 1st and 2nd lumbar), being connected to them by fibrous tissue, except on the left side, where there is bony union between it and the lamina of the 2nd lumbar vertebra.

The spinal cord passes in two divisions on the sides of this process unsymmetrically, as described in the report. The central canal, which is dilated in the upper part of the specimen, is continued into the right or larger division, and a blind tubular pouch projects from it through an interval between the arches of the 12th dorsal and 1st lumbar vertebræ—the arches, that is, of the vertebræ, the bodies of which are united. This pouch is accompanied and surrounded by a process of dura mater, which forms a covering over it. The central canal is not dilated below the bony process. The mass of the swelling into which the pouch projects appears to be formed of soft connective or mucous

tissue, covered by skin or structure continuous with the skin and subcutaneous tissues. That, however, it is not easy to decide in the present state of the specimen.

3. In the specimen in St Thomas' Hospital (No. LL, 12³), described and represented in the same report (the skeleton of a foetus with spina bifida affecting the last dorsal and the lumbar and sacral vertebræ), a cylindrical process bisects the vertebral canal just above the spina bifida, and closely resembles the upper, or azygos, process in my case. It passes backwards (from between the bodies of the 11th and 12th dorsal vertebræ apparently) to the arches of the 10th and 11th, which are pressed together in consequence of a slight curve forwards at the junction of the dorsal and lumbar parts of the column. There is a median depression, giving the appearance of two ossific centres in the fore part of the body of the 11th dorsal vertebra in front, and in that of the 12th behind.

4. In the specimen (No. 3485) in St Bartholomew's Hospital, mentioned in the same report, of lumbo-sacral spina bifida, where a median process extends from before backwards across the vertebra canal, perforating the spinal cord immediately above the spina bifida, there is evidently great irregularity in the bodies of the vertebræ and in the formation of the lower part of the spine.

5. In the specimen in University College (No. 5195), also mentioned and represented in the report as an instance of partitioned spina bifida and bifid spinal cord, with a small process of bone in an antero-posterior direction, crossing the vertebral canal a little above the sac, and lying between the halves of the cord, Mr Topham has been good enough to bisect the spinal column. This shows that the spina bifida commences at the 11th dorsal vertebra, that the bodies of the vertebræ along the whole column are serially and numerically correct, but that the bodies, from 5th to 9th inclusive, of the dorsal vertebræ are small—some smaller than others—and that placed behind these, in close contact with them and dwarfing them, is a second, or supplementary set of bodies or apparent bodies. These are separated from one another and from the bodies in front of them by lines (apparently) of intervertebral substance, as in my own case. Furthermore, at the back of these are three smaller

osseous pieces, also resembling vertebral bodies, which are produced into processes projecting into the vertebral canal, and the halves of the bisected spinal cord pass on the sides of these processes.

The further examination of these four specimens already described in the report above mentioned has disclosed some additional facts; but I do not know that it has thrown any light upon the real nature and morphological relations of the processes which are thus found to project into the vertebral canal in some cases of spina bifida. In all, except that in the College of Surgeons, and the lower one in the first case which I have described, the processes are above the spina bifida. In two, as in my specimen, they are immediately above it; in that in University College (No. 5) they are higher up. There may or may not be some irregularity in the bodies of the vertebræ; and when there is an irregularity it is difficult to see any connection between it and the abnormal processes. The supplementary bodies, or apparent bodies, behind the normal ones, and projecting into the vertebral canal, found in the University College specimen, resemble those in mine; but they are situated above the spina bifida, where the vertebral bodies and arches were in other respects normal; whereas in my specimen they project into the spina bifida.

6. Mr Batteham, house surgeon to the Wolverhampton Infirmary, has been good enough to send me a specimen of sacral spina bifida, taken from a male child, æt. 16 days. It was removed three days after death, when the soft parts were not in a fit condition for minute examination. When I received the specimen it was dry, and the soft structures had been in part removed. After it had been soaked in water I find that the arches of the lower dorsal vertebræ are complete, that all those of the lumbar vertebræ are incomplete, but, as in my case, have their proper direction, and the cord passes normally beneath them. The sacral arches are laterally deflected, giving great width to the vertebral canal at that part. The sacrum appears to terminate abruptly at the second vertebra; but a plate of bone, which is probably a continuation of it, runs horizontally forwards from it between the two iliac bones. There is no trace of coccyx. The lowest part of the vertebral column is there-

fore very imperfect. A median hard bony process arises from the back of the space between the 3rd and 4th lumbar vertebræ, and expands like a T into a transversely flattened plate, which meets, on the two sides, the laminæ of the 3rd lumbar vertebra and completes the arch. A similar process, consisting of cartilage and bone, projects from the back of the bodies of the 1st and 2nd sacral vertebræ. It expands, and, inclining to the right, is connected with the right side of the 5th lumbar vertebra, thus bridging over the right side of the vertebral canal. The spinal cord passes in two divisions, one on either side of these median processes. The right division, passing under the arch formed by the lower median process, is connected with the back of the sac of the spina bifida. That on the left side has been in great part cut away; and all traces of the sac on this side have been removed. It may be inferred that the left division of the cord passed beneath the arch formed by the upper process, and, like that on the right side, reached the sac of the spina bifida.

EXPLANATION OF PLATES XVII., XVIII.

Fig. 1. View of interior of sac of spina bifida from which the right side has been removed. *a*, upper cut edge of sac; *a'*, lower cut edge of sac; *b*, spinal cord (right division of it) passing under the cartilaginous arch of the 1st lumbar vertebra, and expanding upon the under surface of the wall of the sac, with the nerves passing from it, through the sac, to the intervertebral foramina. Some of the nerves penetrate the wall of the sac where it covers the bony projection into the sac. The under wall of the sac is clear from this bony projection. *d*, the lateralised arches of the lumbar and sacral vertebræ; *e*, cartilaginous lump representing the coccyx.

Fig. 2. View taken from the back and right side of the vertebræ at and adjacent to the spina bifida after the soft parts had been cleared away. *a*, the complete cartilaginous arch of the 1st lumbar vertebra. A needle has been passed beneath the curved azygos bar, which passes from the middle of this arch to the middle of the intervertebral substance between the 1st and 2nd lumbar bodies. *b*, the incomplete arches of the 11th and 12th dorsal vertebræ; *c*, the ankylosed arches of 10th and 11th dorsal vertebræ; *d*, the osseo-cartilaginous projection into the spina bifida; *e*, lateralised arch of 1st sacral vertebra.

Fig. 3. View of section of column. *a*, cartilaginous arch of 1st lumbar vertebra; a bristle is placed beneath the azygos bar. 1, 2, 3,

4, 5, bodies of the five lumbar vertebræ, with the supplementary bones (vertebral bodies and arches?) situated above (behind) the bodies of the 3rd and 4th lumbar vertebræ, and forming the osseo-cartilaginous projection into the spina bifida; *b*, cartilaginous knob representing the coccyx.

Fig. 4. External view of specimen in College of Surgeons.

Fig. 5. Sectional view. 11, 12, 1, 2, 3, the bodies of the lowest two dorsal and the upper three lumbar vertebræ; *a*, the band of cartilaginous intervertebral substance encircling the fused bodies of the 12th dorsal and 1st lumbar vertebræ. The bony process is seen projecting backwards from between the 1st and 2nd lumbar bodies, its hollowed posterior part presenting in section a bifid appearance; *b*, central canal of spinal cord; *c*, tubular prolongation of it between the arches of the 12th dorsal and 1st lumbar vertebræ, covered by an extension of the dura mater; *d*, upper and lower cut ends of the smaller division of the cord, which passed on the left side of the osseous process.

ON THE PENTADACTYLOUS PES IN THE DORKING FOWL, A VARIETY OF THE *GALLUS DOMESTICUS*, WITH ESPECIAL REFERENCE TO THE HALLUX.

BY JOHN COWPER, *Student of Anatomy, University of Edinburgh.*

IN the common fowl, as is well known, the foot possesses only four toes, but in the breed known as the Dorking, there are normally present five digits on each foot. In Tegetmeir's standard work on poultry (p. 92) the following statement relating to this bird is found:—"The feet must be five-toed, the extra toe well developed and distinctly separated from the others."

I have dissected the feet of four specimens of this fowl, with the view of determining the arrangement of the extra toe. The tarso-metatarsus is divided inferiorly into three articular surfaces for the three outer digits, and, as in other birds possessing more than three digits, there is also present a rudimentary 1st metatarsal bone, articulating with or attached to the lower end of the inner aspect of the tarso-metatarsus. It is with the distal part of this bone that the toe which it is customary to call the hallux articulates. In the case of the Dorking the rudimentary 1st metatarsal bone presents, however, two distinct articular surfaces on its distal aspect, the inferior and smaller of the two being for articulation with the so-called hallux, while the superior and larger is for the proximal phalanx of the extra digit normally present in the Dorking fowl. This digit is almost exactly on the same antero-posterior plane as the so-called hallux, but is placed superior to it. The so-called hallux possesses two phalanges, while the extra toe possesses three, which latter are usually larger than those of the so-called hallux, and the distal phalanx of the extra toe carries a claw, just as does the corresponding phalanges of the other toes.

On the dorsal aspect of this extra toe a tendon is situated, which is inserted into the proximal end of the dorsal aspect of the middle phalanx, and it may be also into the terminal

phalanx, by means of a prolongation ; the tendon, when followed up, is found to take origin opposite the upper end of the tarso-metatarsus, from the common extensor tendon of the three outer toes—this latter tendon coming from a muscle situated on the anterior aspect of the crus. The so-called hallux possesses an extensor tendon, which is seen to be derived from a muscle arising from the anterior aspect of the upper end of the tarso-metatarsus. It has also a flexor tendon inserted into the proximal end of the inferior aspect of the proximal phalanx, which is derived from a muscle arising from the inner aspect of the upper end of the tarso-metatarsus. There is also a second tendon inserted into the terminal phalanx on its inferior aspect, and this tendon is common to the so-called hallux and the extra digit; it is derived from a muscle of the crus, and bifurcates, one half going to be inserted into the inferior aspect of the terminal phalanx of each of these toes; just before bifurcating it sends tendinous slips to the flexor tendons of the three outer digits. This extra digit is truly transmitted, so much so that it constitutes one of the essential characteristics of the Dorking fowl, and it is stated in Mr Darwin's *Animals and Plants under Domestication* to be generally transmitted to the offspring, even when crossed with other breeds which only possess four toes.

What is the morphological value of this extra toe?

Professor Huxley states, in his *Anatomy of Vertebrates*:—

In all birds, even in Archæopteryx, the 5th digit of the pes remains undeveloped, and the 2nd, 3rd, and 4th metatarsals are ankylosed together.

Professor Owen states, in his *Comparative Anatomy and Physiology of Vertebrates*, vol. ii. p. 83:—

The toes of birds never exceed four in number, and of these three are usually elongated and directed forward, diverging, while one is short and directed backward. The hind toe articulates on the same plane as the others in grasping and perching birds, but on a higher level in terrestrial and aquatic kinds. By the analogy of the number of the phalanges of these toes with those in lizards, the back toe is the innermost, answering to "hallux," the inner of the front toes is the 2nd, the middle one is the 3rd, the outer one is the 4th; it will be seen that the number of phalanges progressively increases from two to five. The 5th toe of the four phalanges in the Monitor is not developed in any bird.

In the foot of the Dorking fowl I believe that the toe second in position and possessing two phalanges represents the so-called hallux of other four-toed birds, because it occupies the same morphological position, has the same number of phalanges, and articulates with the rudimentary metatarsal placed on the inner aspect of the tarso-metatarsus. If then the extra toe, possessing three phalanges, and placed internal to the so-called hallux, is to be regarded as a constituent part of the formation of the foot, and not as a monstrosity—and its constant presence in the Dorking's foot is, I think, sufficient evidence that it is not a monstrous formation—then it, and not the digit usually called "hallux," occupies the position of the hallux, and must be regarded as such. If this be so, it follows that the so-called hallux, possessing two phalanges, is really the 2nd toe, and that the toes usually called 2nd, 3rd, and 4th, are the 3rd, 4th, and 5th; the missing toe in a four-toed bird being not the 5th but the hallux, and the so-called hallux being the 2nd toe. In such a case, the rudimentary metatarsal, with which the 1st and 2nd toes of the Dorking fowl articulate, probably represents the elements of the 1st and 2nd metatarsals, and the tarso-metatarsus represents the 3rd, 4th, and 5th metatarsal bones.

Taking the Reptilia as a class, they possess five digits in the pes; in the Mammalia, however, the digits of the pes are very commonly reduced in number, and Professor Flower states—"if one toe only is absent it is the first or hallux," so that, if the above view of the morphology of the foot be correct, the bird follows the mammalian rule in this respect.

THE VITALITY OF WILD ANIMALS UNDER FIRE.

By Brigade-Surgeon WILLIAM CURRAN, A.M.D. (PLATE XIX.)

THE comparative immunity with which soldiers and others engaged in warfare receive wounds in vital parts is well known. Many instances of this immunity are on record, and specimens in point may be seen any day in our leading anatomical museums. They are also described in great detail by surgical writers, but the particulars of these would be unsuited to these pages, and the books containing them are open to all. It is not so well known that our fellow mortals, "the beasts that perish," are equally favoured in this respect, and one would look in vain, even through the writings of professional veterinarians,¹ for any exhaustive account of this immunity. We therefore think that the matter stands in need of elucidation, if only from an artistic point of view, and what we have to say on the point is fortunately based on our own personal experience, or on the statements of friends whose competence and veracity are beyond the reach of doubt.

It would not be easy to say what species of animal exhibits the largest amount of this kind of tolerance, nor has the question been, so far as we know, ever raised. Anyhow, it has not been determined, and, even admitting that a comparison is possible, it is not easy to see how one could be instituted, with any approach to accuracy, between the heart of a whale, which fills a large tub, and that of a mouse or a weasel that can be taken up on the end of a pin or swallowed at a bite by a small puppy. All we need say is that as "the structure of the lungs, the mechanism of respiration, the arrangement of the pulmonary vessels, the cavities of the heart, and the general disposition of the arteries and veins of the systemic circulation, differ in no material circumstance (in the Mammalia generally) from what is met with in our own persons," so also there would be no more

¹ Williams's *Veterinary Medicine* (p. 519) is the only work that contains, so far as we know, any information of this kind.

difference in this respect between man and beast than their respective sizes, endurance, or muscular development would naturally enforce or imply.

And this, too, is found in practice to be really the case. For though the tiger, the bison, the deer, and other creatures of that kind may exhibit greater momentary activity after wounds in their hearts than man usually does, yet is this their activity not sustained. Their ungovernable rage, fear of man, or efforts at escape only tend by stimulating the circulation, or preventing the closure of their wounds to aggravate the latter, and we find, accordingly, that whilst some wounded beasts are often able to execute fierce charges after they are fatally stricken, or that they can run considerable distances without betraying any sign of vital failure, yet do they as assuredly succumb in the end, and that, too, in a shorter time than their wiser or less impulsive fellow-sufferer—man. But then the latter is not obliged to fly for his life as the beasts are, and that, we fancy, makes all the difference in the case.

Owing to the bungling of a certain executioner in this country, or to the facial contortions of persons beheaded in France, we have lately had discussions in the Press as to the best or least painful method of taking away the lives of our criminals. Some writers advocate the use of prussic acid or other instantaneously fatal poison, others prefer electricity, and a few have suggested chloroform or some similar narcotic. In other words, the advocates of these measures imply that the best means of effecting their purposes are such as operate through the brain and the nervous system, or through the heart—the central organ of the circulation. They want to destroy the sensibility of the one, or paralyse the action of the other, but life is not thereby necessarily extinguished in either case, and it is now generally admitted that consciousness survives decapitation by the guillotine.

On the other hand, very awkward accidents have followed the use of the rope through inexperience, timidity, or intemperance on the part of the executioner, so that measures directed to the stoppage of the heart would seem to be those that make the strongest appeal to our sympathies. But are there any such measures, or is it quite so certain that the cessation of the heart's

action necessarily entails death? We know as a matter of fact that such is not the case, and that many persons whose hearts had ceased to beat to all outward appearance during periods of so-called suspended animation—catalepsy, &c.—have subsequently recovered, and lived long afterwards. *Per contra*, life would seem to survive, if we are to believe hagiologists and others, the actual removal of this organ from its owner. Thus Burnet,¹ describing the execution of one Hackston a covenanter, says that "his heart when cut out continued to palpitate some time after it was in the hangman's knife," and Bishop Challoner² adds that Edward Jennings "uttered the words *Sancte Gregori ora pro me*, after his bowels had been thrown into the fire, and his heart had been torn out by the executioner." Facts of like import are mentioned by toxicologists,³ and the very structure of this organ, consisting as it does of involuntary muscular fibre, would seem to imply that life may coexist with, nay, may even be restored, after it had apparently ceased to act.

Let us now take the heart of a sheep—a very accessible object by the way—and compare with it, as with a standard, the lesions or injuries which the hearts of some other animals are able to bear without immediately failing. It would be readily seen that this is a perfectly healthy organ, very like that of man, though somewhat smaller, and that it possesses substantially the same structure and elasticity as his. One would suppose that any leak, however small, in this central fountain would prove necessarily, if not instantaneously, fatal. But such is not the

¹ *History of his Own Times*, p. 338. He notes, as "a matter of no small astonishment," in his *History of the Reformation*, vol. i. p. 533, that Cranmer's heart remained "entire and not consumed among the ashes" that were produced by the burning of his body. This organ often survives, we believe, the decomposition of the other fleshly parts of its receptacle.

² *Martyrs to the Catholic Faith*, p. 182. Bacon mentions, in his *History of Life and Death*, that "he saw the heart of one that was bowelled for high treason leap, on being cast into the fire, a foot and a half high, and after, by degrees, lower and lower, for the space, as he remembered, of seven or eight minutes." We may put any construction we like on such narratives, and it was stated in a pamphlet of the day that when the body of Bellingham (who was hanged for the murder of Mr Percival in 1812) was dissected, "it was noticed that his heart continued its functions for four hours after he was laid open."

³ See, for a very interesting case in point, Dr Chevers' *Manual of Medical Jurisprudence for India*, pp. 645-7; and Taylor adds that "Duval saw the heart of a criminal, a quarter of an hour after decapitation, beating with great distinctness."

case, and considerable portions of its body may be taken away without apparently diminishing the activity of its owner, or instantaneously extinguishing life. We will now endeavour to establish the truth of this statement by facts drawn from our own or other's experience.

One day, while shooting with a friend near Lucknow, we came across a small herd of the Black Buck or Antelope of the plains. One of these, a female, fell to the rifle of our companion, and as this succumbed to a wound of the head, we subjoin a sketch of its heart, which, it will be at once noticed, was quite intact. The black spot or star on it is intended to show the place in which one of its fellows was struck, about the same time, by ourselves.¹

This latter ran, after receiving our fire, for fully 40 yards or so, as if there was nothing the matter with it, and then rolled over, "all of a heap," and fell dead. Till this took place we were under the impression that we had missed it. On examining its heart afterwards we easily put our forefinger quite through its centre (fig. 1). The ball which inflicted the wound was a sharp-pointed conical one, and was fired out of one of Sharp's patent rifles.

The animal (*Felis tigris*) whose heart is here reproduced (fig. 2), was shot by us at night, while watching from a muchān (a stage in a tree), a buffalo that was tied, as a bait, beneath us, and which it had sprung upon and killed. We fired from a distance of forty paces, but the tigress did not acknowledge our shot, as is usual in such cases when they are struck, but gave one bound and disappeared. We naturally thought that we had missed her, and knowing that our shot and its smell, &c., would effectually scare away any other beast that might be prowling about in the neighbourhood, we retired to our tent for the night. On returning to the spot whence we had fired on the previous night, early on the following morning, we found her lying quite dead, about 120 yards from the same.

¹ This tolerance is not peculiar to the Antelope of India. Mr Myers found a very similar amount of vitality in one of its fellows in Africa. Describing his adventures in a portion of that Continent, he says (*Life among the Hamran Arabs*, p. 215) that "an Antelope, in whose side such a hole had been made that the lung protruded, not only survived for some time, but actually ran away"; and he adds further on, that "a Gazelle managed to gallop off more than one hundred yards after most of its interior had been knocked out by a low shot with an expanding bullet." It has not been considered necessary to include this sketch in our plate.

She had, meanwhile, bitten her thighs through in two or three places, but this is not a very uncommon occurrence, and we have even heard of an instance in which a wounded tigress worried her own young ere she died. The fatal wound was just behind the shoulder, and after skinning her we opened, as was our wont, her chest. The heart was completely shattered, even more so than in the drawing. The ball we used was a spherical gauge, and was fired from a smooth-bore barrel which contained 5 drams of powder.

The heart here figured is that of a panther (*Felis leopardus*), and its owner was killed in much the same way as the tigress just referred to (fig. 3). Our bait in this instance, however, was an old sheep, and not a buffalo, and we fired from a distance of only 5 or 6 feet. The brute bounded away with a growl (a good sign), and we found it dead the next morning about 40 yards from where we stood. On examination the heart was found to be shattered. Our projectile on this occasion was a copper bottle No. 12 bore shell, filled with chlorate of potash and sulphuret of antimony, and it was propelled by 4 drams of powder.

So far, omitting minor episodes, for our own personal experience on the point; let us now turn to the experience of companions or others whose feats we either witnessed ourselves or had them rehearsed to us, *viva voce*, by their authors. A field officer of our acquaintance (a noted Shikāri), answering a recent interrogatory of ours, says:—"I once fired into a full-grown tigress that had been badly wounded in the belly the previous day, as she was going full split in pursuit of prey. My rifle was a 16 bore, and this contained a conical (Jacob's) shell of about an ounce and three quarters weight. It did not explode, which was due, I think, to the fact that I fired broadside on, as she was about 1 foot from my muzzle. I fired from her left side, and (being 6 feet high) directed my aim heartwise, and the ball tore away a good sized piece (of flesh) from the apex of her heart from above downwards."

She then passed on as if untouched, chased for 15 yards or so a gun-carrier, and pulled him down. She continued to worry him alive while I was reloading from the muzzle one barrel, and then sank back quietly all at once *with the man in her mouth*.

He further describes the charge of a full-grown tiger, whose heart had been "smashed to smithereens" by a shell explosion within his chest, and concludes by saying that "I have seen several black-buck, that were shot through the heart itself, go full tilt as if untouched, and then roll over dead."

And *à propos* of the leading passion strong in death, as well in beast as in man, I may be here permitted to interpolate a fact in this connection that was related to me several years ago by a bystander. It runs to the effect, that an officer who subsequently achieved a high position in the service was carried bodily from the houdah of an elephant, at a spring, by a tiger through whose heart a bullet was subsequently ascertained to have passed. The officer in question was deposited on the ground badly bruised and scratched, and was only released from a worse fate by the death of his assailant on his body.¹

And though these statements are sufficient of themselves to establish the truth of our thesis, yet have we considered it desirable to add, as far as in us lay, to their cogency. We have applied with this view to two medical friends, both well-known shots, to favour us with their experience on this point, and they have answered us in confirmatory terms. One of them, an officer of long standing in the Indian Army, assures us that he was once charged by a panther, "the whole of whose thoracic viscera—including, of course, the heart—had been torn to pieces," while on another occasion a *nylghaie* (a species of cow), whose right auricle and root of aorta were wounded by a No. 12 spherical bullet passing through them, went away "for more than 100 yards as if there was nothing the matter with him."

The other, an old friend and *confrère*, writes to us as follows on the same subject:—"I can give you two instances (of survival after gun-shot injuries of the heart, &c.), one shot through the heart with a large shell, and the other shot through the aorta,

¹ We may quote, in corroboration of this fact, the observation of Major Shakespear (*Wild Sports of India*) to the effect that "those who have not actually seen it will scarcely credit that a tiger will often go in his charge several yards, with all the power and capability to strike down everyone in his path, after the bullet has gone through his heart or crashed through his brain." Describing his adventures in South America, Mr Masters says (*At Home with the Patagonians*, p. 53), *à propos* of the Puma, that "to kill this animal with a gun is rather a difficult matter, as, unless the ball enters his skull, or strikes near the region of the heart, he has as many lives as a cat."

close to the heart, by a bullet, which clean divided this vessel in its entirety. The first was a tigress, which stood about 20 yards from me; the shell entered just behind the right shoulder, passed through both ventricles of the heart, and emerged behind the other shoulder. The beast ran a little over 100 yards and then dropped dead."

"B—— shot a tiger with one bullet through part of the shoulder and brisket, and with the other through the right shoulder and aorta as it ran away. This brute gave no sign whatever of being hit, and my friend thought he had missed him, but it was not so; on following up the track we found him dead about 40 or 50 yards ahead of us. I made a *post-mortem* examination in both these, and can vouch for the truth of what I have written," and it is painful to add that these two officers are now dead. One of them succumbed to injuries that were inflicted by a tiger in the Nepal Terai, the other died of a fever that was contracted, in the pursuit of game, in the same locality, and both were men of much promise in their respective spheres.

We might easily adduce similar records in respect of the Himalayan bear,¹ the bison of the American Prairies,² and the ovis ammon, or wild sheep of Thibet, and the Sevāliks, did space so allow. But it does not. We have, we fear, already trespassed too far on the indulgence of our readers, and moreover we have had no experience of our own in connection with these animals. We prefer, therefore, leaving our case to rest on its own merits, such as they are as above, rather than encumber it with details for which we cannot ourselves personally vouch. Books of sport and hunting adventure are common enough, and such of our readers as desire further information on these points may be referred to the writings of Dunlop, Kinloch, Markham, and others, who have specially dealt with this phase of the question.

¹ Sir Edward Melville wonders (*The Last of the Arctic Voyages*, vol. i. p. 64) that a bear he met in Melville Bay showed fight "even after a ball had passed through his brain."

² See Ruxton's *Adventures in Mexico and the Rocky Mountains*, p. 268, and Captain Trench Townshend's *Ten Thousand Miles of Travel, &c., &c.* The writer has been recently informed, by an officer who served at the Cape, that "a bustard once flew (in his presence) several hundred yards after he had received in his chest the contents (buckshot) of a heavily loaded gun, which caused the viscera of his thorax to protrude,

EXPLANATION OF PLATE XIX.

Fig. 1. Heart of the black buck of the plains of India, showing wound in the right ventricle.

Fig. 2. Heart of a tiger, in which the greater part of the ventricles was shot away.

Fig. 3. Heart of a panther, the ventricles of which were destroyed by a 12 bore shell.

THE ALIMENTARY CANAL AND PANCREAS OF
ACIPENSER, *AMIA*, AND *LEPIDOSTEUS*. By
A. B. MACALLUM, B.A., *Fellow of University College,*
Toronto, Canada. (PLATE XX.)

THE investigation, some results of which appear in the present work, was begun two years ago, with the object of treating fully of the digestive organs of fishes in general. Since I have now had for some time but few opportunities for continuing the research further, and do not expect to be more fortunate in this respect for a year or so to come, I have been led to abandon that object wholly. The results of my studies, however, so far as they relate to Ganoid fishes, seem to me to have some value, and I have therefore decided to publish them.

The description here given, so far as it pertains to *Lepidosteus*, is based on forms of 7-10 cm. in length, which I was forced to accept for the purpose, since the adult forms are to be obtained from remote places only, and always in a poor state of preservation for histological examination. As a full description of the histology of the intestinal tract in young *Lepidostei* would not correspond in every respect to the conditions obtaining in the adult forms, I have endeavoured to omit references to peculiarities of structure such as may be affected by age.

The terms fore-gut, mid-gut, and hind-gut are here employed for the purpose of description, as they answer to the conditions of the alimentary canal in fishes better than any others that can be suggested. They have already, to a certain extent, been sanctioned by usage, since they are employed in the English edition of Gegenbaur's *Elements of Comparative Anatomy*.

FORE-GUT.

Œsophagus.—In *Acipenser*, that part of the alimentary canal lying behind the branchial chamber, and terminating about 3 cm. behind the membrane separating the pericardial and peritoneal cavities, is usually considered to be the *œsophagus*. It is comparatively short, and is at once recognisable by the large number of papillæ arranged in longitudinal series on its inner surface.

In its wall are found the two layers of striated muscular fibre, commonly present in the œsophagus of fishes.

There are, however, elements in the structure of this part of the alimentary canal which throw some doubt on its being homologous with the œsophagus of other vertebrates. It is lined with an epithelium formed of many layers of fusiform, polyhedral, or flattened cells, which do not differ to any appreciable extent from those of the membrane lining the posterior part of the pharyngeal chamber. This kind of epithelium is rare in the œsophagus of fishes.¹ There are also to be found in this part taste-buds, occurring usually on the summits of the papillæ already referred to. I have never seen any reference to the occurrence of such structures in the œsophagus of any vertebrate,² but they are to be met with commonly in pharynx, especially in fishes. That part of the fore-gut in *Acipenser* immediately following the so-called œsophagus is devoid of striated muscle, and therefore might be regarded as part of the stomach. But this is not a sure method of distinguishing the two divisions of the fore-gut, for if the anterior part possesses glands which secrete a digesting principle, the absence of voluntary muscular fibre is a necessary condition, in order to allow the secretion to perform its function. The anterior part of the fore-gut in *Acipenser* does possess glands of this description, hence the absence of striated muscular fibre from its wall. It will be seen farther on, that the division of the fore-gut into œsophagus and stomach is not very marked in *Amia* and *Lepidosteus*, the passage from one to the other part being at best but a gradual one. That part following the papillated section of the canal in *Acipenser* must be regarded, therefore, as the true œsophagus, and from its structure, as described below, it may be correctly said to terminate a short distance behind the opening of the duct of the air-bladder, near the commencement of the gastric loop.

The papillated portion is then but the posterior extension of the pharynx. Its inner surface is greyish-white, and the few

¹ According to Edinger (*Arch. für Mikr. Anat.*, Bd. xiii. p. 651) a several-layered scale-like epithelium is present in the œsophagus of *Polypterus* and of some Selachians.

² In *Amphioxus* I have, however, determined the presence of taste-buds as far posteriorly in the alimentary canal as the opening of the "hepatic" cæcum.

folds that are present run longitudinally between the series of papillæ. It terminates about 3 cm. behind the pericardial chamber. The epithelium lining it is constituted of from five to ten layers of cells, which are usually fusiform, often polyhedral or squamous, the superficial layer being, however, formed of cylinder and goblet cells almost invariably. F. E. Schulze¹ found the cylinder cells provided with cilia. I am unable to confirm this, although I have studied the epithelium in fresh and in hardened condition. The theca of each goblet cell is of an elongated oval shape and is filled with mucus, containing a large number of feebly refracting granules. Many of the cylinder cells also exhibit a mucigenous transformation of their contents. The basal processes of both forms of cells are exceedingly fine and delicate. The replacement of the cast-off goblet cells, into which all the cylinder cells are metamorphosed, is accomplished by those of the layer next below them.

The taste-buds are not different from those found in the mouth, except perhaps in their slightly more elongated form (fig. 2). Several may be found on the summit of a papilla.

The true œsophagus possesses to the naked eye all the characteristics of the stomach. The colour of its lining membrane is, in the fresh condition, chocolate-red, and its folds pass uninterruptedly, without increase or decrease in size into, those of the stomach. The calibre of both parts of the fore-gut is the same. The only distinctions to be found between them lie in the histological structure of the mucosa. The point of transition between the œsophagus and stomach, as already stated, is near the gastric loop, up to which point the epithelium of the former retains its cilia, while the peptic tubules found in it are somewhat different from those of the loop.

In *Amia* the œsophagus is short, and terminates immediately behind the opening of the duct of the air-bladder. As in *Acipenser*, the inner surfaces of both œsophagus and stomach are alike in every respect when viewed with the naked eye. The folds in both parts are continuous and arranged longitudinally, while the dull reddish tint of the mucosa of the stomach is possessed to some extent by that of the œsophagus. Where one part ends and the other begins can be determined approximately

¹ *Arch. für Mikr. Anat.*, Bd. iii. p. 174.

only, the lining epithelium and the glands of the anterior part passing without any abrupt change into those of the posterior. Taking the presence of striated muscular fibre as a guide in this determination, although a very uncertain one, the two parts may be divided as œsophagus and stomach at the point intimated.

In *Lepidosteus* the œsophagus commences immediately anterior to the opening of the air-duct; where it terminates posteriorly it is difficult to say. The distinction between the two parts of the fore-gut is not less indefinite, perhaps more so, than in the other two genera. For a third of the extent of the straight tube forming the fore-gut, the epithelium in character and the glands in both character and number differ considerably from the corresponding structures in the posterior two-thirds, although, so far as the glands are concerned, the transition from one to the other part is a gradual, not an abrupt one. The anterior third, which may therefore be termed the œsophagus, does not seem to have any striated muscular fibre in its outer wall, but the specimens from which my preparations were taken were not of such an age as to allow me to speak with certainty on this point.

The opening of the air-duct in *Amia* and *Lepidosteus* is a longitudinal slit on the dorsal side of the œsophagus. This opening is provided with two folds, one on the right, the other on the left, which can be approximated by the striated muscular fibre present in them to shut off, after the fashion of a glottis, all connection between the duct and the cavity of the œsophagus. The muscular fibre is very abundant in *Amia*, in which it radiates out over the duct and on the surface of the air-bladder. In *Acipenser*, in which the opening of the duct is funnel-shaped, there is apparently no mechanism by which the cavity of the air-bladder can be completely closed off from that of the œsophagus.

In *Acipenser*, *Amia*, and *Lepidosteus* the epithelium of the œsophagus is ciliated. The cilia in the first named form a thick brush on each cell, and all usually matted together by mucus; in the other two genera they are much longer and finer. The cells in all are cylindrical, with fine basal processes which pass into and are interwoven with the connective tissue of the mucosa. In *Acipenser*, in the outer or peripheral halves of a large number of these cells, the contents are swollen like those

of the goblet cells, but the staining with various dyes is uniform in the inner and outer cellular portions, the absence of mucigen being thereby shown. In *Amia* many of the cells have lost their cilia and are changed into goblet cells; this is more commonly the case in the shallow crypts which are to be found abundantly over the mucous surface. All the cells exhibit the mucigenous transformation. In *Lepidosteus* the cells are of regular form, with their outer portions containing a quantity of mucigen. Cilia were observed on all the cells. In this genus, as well as in *Acipenser*, some of the cellular elements must, before they break up or are destroyed, open peripherally to discharge their mucus.

In the opening of the air-duct in the three genera the cylinder cells are short, and in the middle of the extent of the duct they become cubical. In *Lepidosteus* the folds at the side of the opening are covered with short columnar cells.

In *Acipenser* and *Lepidosteus* the derivatives of the epithelium in the œsophagus may be referred to three forms:—(1) elongated crypt-like insinkings; (2) elongated crypts terminated in dilated sacs; (3) true gland tubules. In *Amia* in addition to these three classes of structures there is a fourth, examples of which are to be found in the neighbourhood of the mouth of the air-duct, in the latter and even in the air-bladder.

The elongated crypt-like insinkings of the epithelium are apparently most common in *Acipenser* in which they are specially noticeable at the commencement of the œsophagus. They are not always straight in their course through the mucosa. The ordinary epithelium of the general surface is continued into them for half their length, while the lower half of the cylinder cells, though still retained, are shortened, much so in *Amia*, and their cilia less prominent. In these the nuclei are placed next the membrane of connective tissue surrounding the crypt; the contents of the central portions of the cells appear to be mucigenous when viewed in sections of the hardened tissue, but when observed after isolation in serum the mucigen is obscured by the presence of fatty matter in the form of minute globules, which are more abundant near the lumen. In *Amia* the corresponding cells are shorter and the central half of each is packed full of granules, whether of

zymogen or not I am unable to say. In *Lepidosteus* these insinkings of the epithelium are found only at the posterior end of the first third of the fore-gut, and their cells are much shortened, often reaching a cubical form.

In *Acipenser* these crypts may branch more than once, although as a rule they do not branch at all. In this genus they are not found farther than 2 cm. behind the commencement of the oesophagus, where they become changed into the structures of the third class mentioned above. This change is a gradual one, the cells at the bases of the crypts, as the latter are followed backward, becoming shorter and more cubical, assuming at the same time a more specialized glandular character. In *Amia* also, these insinkings are least numerous where the true gland tubules are most so, and passage-forms between the two classes of structures are present.

Elongated crypts terminating in dilated sacs are not numerous in *Acipenser*, and *Lepidosteus* and in *Amia*, in which they appear to occur in the largest number, they bear a very small proportion to the structures of the first class. As to their character they are most highly developed in *Acipenser* and least so in *Lepidosteus*. The tubular part is lined with cylinder cells which decrease in length as the sac is approached, while the cilia become shorter and less abundant. There is in *Acipenser* a slight constriction of the tubule where it terminates in the sac; at this point the cilia vanish and the cells attain their greatest decrease in height. The cells lining the sac and their nuclei are flattened, but the form never becomes squamous. What little protoplasm there is surrounding the nuclei appears clear and transparent.

Sometimes in *Amia* one or more gland tubules are found to open into one of these sacs. This is the case in young forms particularly. I have not, however, observed a like arrangement in the two other genera, but whether it occurs in them or not these sacs are still remarkable on account of their structure, since they have not, as far as I am aware, been observed in any other fish. Their fewness of number and their limited distribution in *Acipenser* also render them worthy of note. They cannot serve in any case for the purpose of absorption, since they are placed too far in front of the seat of digestive changes,

and as they are undoubtedly devoid of a glandular function, one is compelled to consider them to be transudatory organs. A careful study of the histology of the fore-gut in a large number of fishes may show the presence of these structures to be more general.

True gland tubules are most abundant in the cesophagus of *Acipenser* and fewest in *Lepidosteus*; in the latter they are only to be found at the posterior end of the cesophagus. In the first named genus they are usually much elongated, the elongation increasing as they are followed backward. Large cubical cells line them and enclose a lumen of considerable size. The contents of the central half of each cell stain with difficulty in carmine, while the contrary is the case with the outer half in which the nucleus is placed. The edge of the cell touching on the lumen is very irregular and ragged in appearance, owing to the abundance of granules present.

The neck of each tubule and the crypt into which it opens constitute from one-third to one-half the length of the three parts, and in this respect there is a marked contrast to the glands of the anterior portion of the stomach in *Acipenser*, or to those in any part of the cardia in the other genera. In the crypt the epithelium is the same as that of the general surface, being ciliated and cylindrical. In the neck of the gland the cells are transitional in their form, and contents between those of the crypt and those of the body of the tubule, being nearly cubical in form, and containing a non-granular protoplasm with a narrow zone of mucigenous matter in each, which borders on the lumen.

There is in *Amia*, as already mentioned, a fourth variety of tubules occurring at the mouth of the air-duct, and appearing to be similar in every respect to that found in the air-duct itself, and on the inner surface of the inferior wall of the air-bladder. Tubules of this sort are not numerous. They and the crypts into which they open are very short. Their cells are narrower and shorter than those of the other kinds of tubules described. Sometimes the contents of the cells are strongly granular, at other times they are constituted of mucus almost wholly. The lumen of the tubule is more frequently indistinct.

I had not, unfortunately, an opportunity of studying these

tubules in a fresh condition, when a careful examination of them might reveal more about their function. They are in all probability but degraded forms of the true gland tubules of the œsophagus. A wider knowledge of the histology of the air-bladder in fishes may show that the occurrence of tubules of this description is not confined to *Amia*, since the air-bladder, before its function had become hydrostatic, probably acted as an accessory secreting organ provided with the same histological structure as the fore-gut from which it originated as an out-growth, and ought, therefore, still to have in many cases traces, though rudimentary, of this similarity.

Stomach.—The stomach in the three genera shows a considerable difference of form. The division of it into cardia and pylorus is easily distinguishable, much more so than is the division of the fore-gut into œsophagus and stomach.

In *Acipenser* the stomach is thrown into a loop which extends forward in front of the mouth of the air-duct, where the cardiac portion terminates in a retort-like pylorus. The wall of the cardia does not differ in thickness from that of the œsophagus, but in the pylorus the thickness is from one and a half centimetres, especially at the upper and under surfaces, at each of which the muscle fibre is collected into a thick plate-like mass; this in the relaxed condition of the pylorus lies flat on its fellow of the opposite side. At the right and left borders of these thickened plates the wall of the pylorus is as thin as in the cardia. In the latter the colour of the mucous membrane in its fresh condition is chocolate-red and the folds are arranged longitudinally, while in the pylorus the mucous membrane is dull white and its surface smooth. Viewed from without there is a contrast in the colour of the two parts of the stomach, that of the pylorus being a glistening white. In a sturgeon measuring 66 cm. the cardia was 16 cm., and the pylorus 3 cm. in length.

In *Amia* the cardia is dilated and its cavity is continued behind into a conical cæcum. The pyloric tube originates from the lower side of the cardia and passes forward and outward, undergoing a constriction where it unites with the mid-gut. The wall of the stomach is of equal thickness throughout, except for a slight increase of the muscular tissue

near the termination of the pylorus. The mucous membrane is folded, the direction of the folds being longitudinal; its colour is the same in the first half of the pylorus as it is in the cardia and cæcum. The surface of the membrane in the posterior half of the pylorus is nearly smooth. The colour here is a dull white.

In *Lepidosteus* the calibre of the stomach increases as it passes backward. Its cæcum, if it can be said to have any, is very short. Its mucous membrane is raised into longitudinal folds. On the inferior surface the narrow pyloric tube passes forward a short distance, then turns to the right, and terminates in the mid-gut immediately in front of the lobulated pyloric appendage.

The epithelium of the stomach in *Acipenser* is somewhat different in character from that in the cesophagus, and it differs even in the cardia and pylorus. The cells constituting it in the cardiac portion are longer and more slender than those in the cesophagus, and smaller than those in the pylorus. They are unciliated, a peripheral membrane is present in each, and their contents do not apparently show any traces of that transformation into mucigen usually observable in the gastric epithelium of other vertebrates. The staining in my preparations is quite uniform throughout each cell. Only when Müller's fluid or a solution of potassic bichromate had been used as a hardening reagent did any of the cells, and then only a few, exhibit a peripheral opening. When alcohol alone had been used in preparing the epithelium the peripheral wall of each cell appears thick, probably owing to a deposit of mucus on the outside.

In the pylorus of *Acipenser* the majority of the cells of the epithelium are open peripherally; from this, and from their being sometimes swollen, they bear a resemblance to goblet cells. The contents of the distal half of each cell are almost completely mucigenous. A thick dense layer of mucus is often found to cover the epithelium, but it does not dip down into the crypts, although it accommodates itself to the general surface of the mucous membrane. Scattered throughout this layer of mucus a large quantity of granules together with nuclei of broken-down cells can be observed.

In *Amia* the epithelium is ciliated throughout the cardia,

cæcum, and pylorus. The cells are long and cylindrical, slightly swollen at their peripheral halves, and they are covered in chromic acid preparations by a thin coat of mucus. The contents in the peripheral half of each cell do not appear in fresh condition to differ from those in the central half, but when hardened and stained it is usual to find the outer half of the cell completely uncoloured. The cilia are obscured by the coat of mucus, but in the deeper crypts when this is absent they can be easily observed.

In *Lepidosteus* the epithelium of the posterior two-thirds of the fore-gut is unciliated, except in the posterior half of the pyloric tube. The cylinder cells are always provided with a peripheral membrane. They contain mucigen, as they are stainable only in their central halves.

The glands of the cardia in *Acipenser* are of the type to be usually found in fishes (fig. 7). The crypts of the epithelium, into which several gland tubules may open, have evidently been mistaken by Leydig¹ for glands, and they form, according to him, as such the only kind observable in *Acipenser*. Edinger,² commenting on Leydig's description, remarks that it is doubtful if *Acipenser* has true gastric glands, for the structures figured and described by Leydig bear no resemblance at all to the peptic glands of other fishes. Wiedersheim,³ also misled by Leydig's description, doubts the existence of peptic glands in the Sturgeon. I am unable to explain how Leydig came to overlook the true glands, unless it is that in the species studied by him the epithelial crypts are actually the only approach to the form of glands present. This is not probable, however, and further attention given to the structure of the gastric mucosa in *A. naccarii* and *nasus*, the species employed by Leydig in his research, will in all likelihood show glands not differing to any appreciable extent from those observed by me in *A. rubicundus*.

The cells of the tubules may be classed according as they occupy the neck or the body of the gland. Those in the neck evidently do not secrete pepsin, as they lack granules and gene-

¹ *Untersuchungen über Fische und Reptilien*, Berlin, 1853, p. 16; also *Lehrbuch der Histologie*, 1857, p. 313.

² *Arch. für Mikr. Anat.*, Bd. xiii. p. 651.

³ *Lehrbuch der Vergleichenden Anatomie der Wirbelthiere*, p. 581.

rally take a uniform stain with hematoxylin or carmine. They are transitional in their form and characters between the ordinary epithelial cells and those of the body of the tubule, being similar to the latter in size and shape. In this part of the gland the lumen is distinct in the body, usually it is not. The true gland cells are rhombohedral in shape; the nucleus in each is placed in the half of the cell removed from the lumen, and the contents of the central half are very granular and difficult to stain. In preparations made from a Sturgeon which had undergone previously a prolonged period of hunger, the staining which these cells took was more uniform. Ordinarily they are seen, when isolated, to have each a fine process, which, when the cell occupies its position in the tubule, is directed downwards between the membrana propria and the cell next below. These processes are to be observed in the gastric glands of many fishes, for example in *Perca*, *Amiurus*, *Gasterosteus*, *Stizostedion*, *Esox*, &c., and they seem to point out that the development of epithelial cells into gland cells is not a complete one in fishes, so far as form is concerned.

These glands are more numerous, but shorter near the pylorus. In the pylorus they are replaced by the less numerous mucous tubules, which are very much elongated, and provided each with a wide lumen (fig. 9). The cells constituting them are of two kinds: short goblet cells and columnar cells, the latter being sometimes wholly replaced by the former. The columnar cells are closed and their contents slightly granular. In the goblet cells the greater part of each is formed of a moderately swollen theca, the contents of which are clear, unstainable, and apparently formed of mucigen. The nuclei in both forms of cells are placed next the membrana propria of the tubule. These mucous glands are evenly distributed throughout the pylorus; the replacement of the cardiac glands by them is an abrupt, not a gradual one.

In *Amia* one or more gland tubules may open into each short crypt of the epithelium. As in *Acipenser* the cells of the neck and those of the body of the tubule are quite different. Those of the body are provided with fine processes also. The lumen is distinguishable usually only as a line in the axis of the tubule, but it is seen more clearly in transverse section (fig. 8). The gland cells are small and but slightly granular. Since all my

preparations were made from specimens of *Amia* which had gone without food for nearly two months, I am unable to speak of the condition of these cells during activity. As it is, they and their nuclei stain deeply and nearly uniformly. The cells of the neck are fewer in number compared with those of the body of the gland than in *Acipenser*. In the pylorus they become more numerous at the expense of the gland cells. About the middle of the extent of the pylorus the neck cells form about three-fourths of the tubule, while a few millimetres farther on the gland cells vanish completely. The tubules then in the posterior half of the pylorus are formed of cells, not differing from those in the necks of the cardiac glands except in the greater abundance of cilia.

In *Lepidosteus* the gland cells in the cardiac tubules are small, but their nuclei are large. Granules were not observed in the interior of the cells during either their resting period or their functional activity. Naturally a different result would be obtained in the case of a fully adult form. The cells stain uniformly in carmine or hematoxylin. Mucous glands, such as are figured by Edinger from the posterior part of the stomach, were not developed in the specimens from which my preparations were made. In the shallow cavity answering to a cæcum the few tubules present had a larger lumen than those in the main portion of the stomach, but are shorter in length.

THE MID-GUT.

The mid-gut in *Acipenser* has a different arrangement as regards its coils and loops from what it has in either *Amia* or *Lepidosteus*.

In *Acipenser* the anterior or duodenal portion is a straight tube of about 12 cm. length (in a specimen measuring 66 cm.), and terminates in a median portion of 7 cm., which is directed forward to pass into the posterior, or valvate section of the intestine. The latter portion, which tapers into the rectum or hind-gut, contains the spiral valve. The median part is as a rule of smaller calibre than the others, from which it is marked off by a slight constriction at each end. The valvate part is of largest diameter and provided with the thickest wall. It is supplied with a vein and an artery, both of considerable

size, which accompany the coils of the spiral valve about the axis of the intestine. The course of the two vessels appears usually very distinct through the muscular layers and the serosa, but sometimes the amount of pigment present is such as to obscure them. It is noticeable in the other portions of the intestine, as well as here, that pigment tissue is distributed chiefly along the course of the vascular channels. The valvate portion of the mid-gut measures about 20 cm. while the hind-gut is not more than 1 cm.; the former is also greater in length than the anterior and median sections taken together.

In *Amia* the anterior straight portion of the mid-gut measures 18 cm. (in a full grown specimen of 55 cm.), nearly occupying the length of the peritoneal cavity. It is connected on the left with a median portion of 9 cm., which is directed forward, and terminates opposite the cæcum of the stomach in the posterior part answering to the valvate section of the mid-gut in *Acipenser*, but having a very small portion of itself occupied by the spiral valve. The rectum or hind-gut does not measure more than 2 cm. The spiral valve is 3 cm. long, the total length of the mid-gut in front of it being 32 cm.

In figures of the intestine in *Amia* which have been given hitherto, the mid-gut is represented wrongly with a calibre greatly decreasing as it extends backward. The only decrease in size which occurs at all is to be found in the rectal portion.

In *Lepidosteus* there seems to be a great difference in the number and arrangement of the loops, according to the size of the specimen examined. In young forms it is as represented in fig. 1. Consulting, however, the figure of the intestines, as given by Balfour and Parker¹ in their work on the structure and development of *Lepidosteus*, one sees there a more complicated looping of the mid-gut, which, according to these authors, possesses three compact coils. The specimen of *Lepidosteus* from which their figure was drawn measured 100 cm. I was consequently at first of the opinion that the figure given here represents a very early condition, but such a condition is indicated by van der Hoeven² in a case where the alimentary

¹ *Phil. Trans.*, 1882, pt. i. p. 359.

² "Ueber die zellige Schwimmbase des *Lepidosteus*," Müller's *Archiv*, 1841, and pl. x.

canal measured 30 cm., and, moreover, notes made three years ago, when I was dissecting a smaller specimen, seem to show that this arrangement persists for a large part of the life of the fish.

It is, however, not surprising that great differences should be found in the mid-gut of *Lepidosteus* and of fishes generally. I have elsewhere¹ called attention to the unequal growth of this part of the intestine in *Amiurus nigricans* during its life history. In this fish it was shown that the mid-gut of one of 60 cm. body-length measured more than treble that of a specimen of 38 cm. This disproportion in the growth of the mid-gut, in relation to the growth in length of the body, is noticeable in other fishes also. In consequence, the difference in the arrangement of the loops in the mid-gut in *Lepidosteus* is explained on the ground that an increase in size of the body calls for a greater increase in the length of the principal part of the absorptive tract, which is thereby thrown into a larger number of coils.

The arrangement of the loops in a young *Lepidosteus* is interesting on account of its similarity to that in the mid-gut of *Amia*. It appears probable then that this was the disposition of the parts in the mid-gut in both genera before the spiral valve had acquired its present rudimentary condition.

The pyloric valve in *Acipenser* and *Amia* takes the form of a tube projecting into the cavity of the mid-gut for a centimetre or more. A valve like this is present in *Lepidosteus*, according to Balfour and Parker; it is present in young forms of 7–10 cm. length, but it is not fully developed. In *Acipenser* and *Amia* it is provided with a thickened ingrowth of the fibre of the *muscularis mucosæ*.

The inner surface of the anterior, or duodenal section of the mid-gut in *Acipenser* is covered with a thick mucous membrane honey-combed with crypts of various size, the openings of the majority of which are very plainly visible. There is otherwise but little unevenness of surface. If the membrane is in a bad state of preservation, however, or if its epithelium has been macerated away, it then presents the appearance of a network of minute folds, a condition erroneously ascribed to the intact membrane. In the median part of the mid-gut, that which is

¹ *Proceedings Canad. Inst.*, Toronto, new series, vol. ii. No. 3.

directed forward, the crypts are as a rule smaller and less numerous, while the mucosa apparently is thinner.

In *Amia* the mucous membrane of the anterior section of the mid-gut shows a prominent network of folds, at the junction of every two of which occurs a prolongation outwards in the form of a villus. The surface is uneven, and the crypts visible to the naked eye seem to be but shallow cavities between the folds. As in *Acipenser*, the median portion possesses in its mucosa the characters of the anterior section, but in a less marked degree: its folds are smaller, its surface smoother, and its crypts less numerous.

In my preparations of *Lepidosteus* the mucous membrane is folded alike over the whole of the mid-gut, and presents insinkings of the epithelium to form structures analogous to the crypts in *Acipenser* and *Amia*.

In *Acipenser* the mucous membrane of the valvate section of the intestine is as thick as that of the anterior or duodenal section, but in the size and the number of the crypts it is like that of the median part. The crypts are all but absent from the surface of the spiral valve. In *Amia* the corresponding section of the mid-gut is in its anterior two-thirds lined with a mucosa of a character like that of the median portion which is directed forward. In the posterior third, containing the spiral valve, the mucosa of its wall, between the threads of the spiral, is provided with narrow longitudinal folds, oblique, or transverse ones being wanting. The larger crypts visible to the naked eye, occurring on the spiral valve, which is almost as smooth as in *Acipenser*, are very few in number and may be completely absent.

The number of turns in the spiral valve in *Acipenser* is usually eight, and the distance between them averages about 2.5 cm. The valve appears sometimes thin and membranous, at other times it is found to be very thick, the difference in size being no doubt due to the degree of distension to which the lymph- and blood-vessels are subjected. This portion of the intestine is always provided with a thick and unyielding muscular wall.

In *Amia* the spiral valve makes nearly four turns. It is not as thick nor as high as in *Acipenser*, and the turns of the spiral

are more closely approximated, being about three-fourths of a centimetre apart.

In *Lepidosteus* the valve makes three and a half turns, and in specimens of 7-10 cm. in length is so large as to fill completely the lumen of the intestinal tube. There is evidently a reduction in the number of turns of the spiral in advancing age, for, according to Balfour and Parker, in the fully adult specimen examined by them the valve does not complete the second turn.

A transverse section of the anterior portion of the mid-gut in *Acipenser* shows under the microscope a mucosa crowded with elongated crypts or tubules, each possessing a large lumen of varying diameter. They may open separately on the epithelial surface, or several may be united so as to open by a large common mouth. They are a continuation of those of the pylorus, but have acquired a differently constituted epithelium, which is, however, the same as that of the ordinary surface of the anterior part of the mid-gut. It is formed of one layer of cylinder cells, but there are at least two layers of nuclei observable (fig. 11). The nuclei of the lower layer are those of young cells destined to replace the cast-off or waste cells above them. The superficial cells have granular contents, often holding also fatty particles, and they possess a hyaline peripheral wall surmounted by a short fringe of cilia. The latter are to be observed only in carefully preserved material, and then they present very often the appearance of a coat of mucus on the ends of the cells. Goblet cells are not common.

In *Amia* a somewhat different appearance is presented by a transverse section of the anterior part of the mid-gut. Here the tubules densely crowding the mucosa are very much elongated, rarely branch, and radiate straight outward from the epithelial surface. These, as well as the epithelium, are constituted of short cylinder cells resting on four or five layers of nuclei. The cylinder cells are, apparently all of them, closed peripherally, and are fringed with strong cilia. It is impossible to trace in hardened preparations the outlines of the cells for more than a third of the depth of the epithelial stratum, the cause of this difficulty being the granulation and the extreme abundance of nuclei which are no doubt those of young cells.

The adenoid tissue of the mucosa is very scanty between the tubules, this being specially the case in *Amia*.

In *Lepidosteus* the tubules of the mid-gut are, in my preparations, but wide-mouthed pouches clothed with cylinder cells, having only one series of nuclei. The cells are longer and slenderer than in *Acipenser* and *Amia*, with delicate, often not detectable, cilia. Goblet cells are common; they occur very often in an exhausted condition; the body of the cylinder is more slender than usual, a small portion of the peripheral end remaining swollen and containing mucigen.

The histological relations of the median portion of the mid-gut in *Amia* and *Acipenser* are the same as those of the anterior portion. In the section containing the spiral valve in both genera, the epithelium is different in some respects, and the tubules fewer and shorter, while the adenoid tissue of the mucosa is more abundant. Goblet cells are more common, and the cylinder cells larger and more granular in their contents, the cilia also being longer and thicker.

In *Acipenser* the epithelium of the spiral valve is constituted, one-third at least, of goblet cells. The cylinder cells are very much elongated, and if observed in fresh condition they usually appear charged with fatty granules. Their peripheral ends are closed by a hyaline wall, covering which is a long brush of cilia¹ (fig. 13).

Many of these cells, when isolated carefully after maceration, show very fine processes which are sometimes dendritic at their terminations. The fact that the processes, more frequently appear to be divided than is the case with other epithelium of the alimentary tract, may be due to the greater ease with which they are isolated from the fibrous tissue of the mucosa, without injury or breakage. The outer halves of the goblet cells are much inflated. Their transformed contents are very granular, and project beyond the epithelial border in the form of a stopper.

In *Amia* and *Lepidosteus* the epithelium of the spiral valve does not differ from that of the neighbouring intestinal wall.

¹ According to F. E. Schulze these cells are provided with striated outer borders. It is possible that what was taken by this observer for a striation was in reality a fringe of cilia. I have been unable to find the original description by Schulze, and only saw a reference made by Edinger to it.

In *Acipenser* the tubules of the spiral valve are comparatively few in number and usually very short. The majority of them are but shallow insinkings of the epithelium, and in all of these goblet cells are very numerous. There are others, however, which differ somewhat from them, although a further study of fresh material may show both forms to completely resemble one another. Such tubules, of which but very few were seen, open into shallow pouches of the epithelium, and being much elongated they sometimes reach through half the thickness of the valve. They lack goblet cells. The fringe of cilia is much shorter and finer than that of the ordinary epithelium. Whether these structures are the representatives of the tubules in the anterior part of the mid-gut and in the neighbouring intestinal wall I do not know. They are probably derived from the latter, and if the present description of them is correct they form a class of structures which are unique in themselves, and in all likelihood perform the functions of the Lieberkühnian glands in higher vertebrates. In *Amia* I have not found similar structures on the spiral valve, the tubules and crypts of which are alike in every respect to those found on the ordinary intestinal wall.

In the axis of the spiral valve in *Acipenser* and *Amia* there is present a large quantity of unstriated muscular fibre, which in the last-named genus is aggregated into a single bundle. In *Acipenser* there are several bundles, arranged irregularly in direction and position. In vertical sections of the valve they sometimes appear separated by large lacunar spaces, which probably are the parts of lymph channels. At other times a muscular bundle appears almost surrounded by a closed follicle filled with leucocytes. In every case the bundles are distinctly marked off from the adenoid tissue of the mucosa. Scattered so irregularly as they are through the valve, it is almost impossible to conceive that they represent excessively developed portions of the *muscularis mucosæ*.

Lymph follicles are very abundant in the spiral valve of *Acipenser*, as many as seventeen having been counted in a single vertical section. They are usually round or oval in shape when near the epithelium, but of irregular form when nearer the centre of the valve, and always of varying size. When very numerous

the valve appears to be made up in bulk almost wholly of them. Sometimes they are placed so near to the epithelium that the latter appears to rest immediately on them. Around each follicle ordinarily the connective tissue is collected into a dense sheath, in which one can observe a number of corpuscles (fig. 14). The structure of the interior of the follicle can be made out only after the greater number of its cellular elements are removed, and this is accomplished by well agitating a thin section of the valve in water. Then, when stained, the close fibrillar network comes out clearly in the interior of the follicle, which still contains a few lymph corpuscles in the meshes of this network. At the same time, too, there can be seen in transverse section a large number of arterioles scattered over the field of the follicle.

Hyrŧl¹ observed in the axis of the spiral valve in *Acipenser ruthenus* a large compact lymphoid organ, which he considered to be homologous with a similarly situated structure in *Lepidosiren*. Ayers² has found lymphoid capsules in the same species, and has given a figure of a vertical section of the valve to compare as to these capsules with one of the valve in *Lepidosiren*. They are undoubtedly homologous structures, although the anterior part of the organ in *Lepidosiren*, found outside the intestine, is lacking in *Acipenser*. A compact organ such as Hyrŧl observed does not exist in *Acipenser rubicundus*, in which lymphoid follicles are more highly developed than in the species used by these authors for investigation.

Scattered collections of lymph corpuscles are very common in the various parts of the intestinal tract in fishes, and as such they simply represent an overloading of the adenoid tissue of the mucosa and submucosa with these structures, the limits of the deposit being rarely sharply definable. A compact lymph organ has been observed in the œsophagus of some Selachians, and, according to Edinger,³ who has given the most detailed account of it, it possesses a capsule of connective tissue, from which trabeculæ of fibrils penetrating the interior divide and redivide,

¹ "Lepidosiren paradoxa," *Abhand. der böhm Gesell. der Wiss.*, 1845. I have had no opportunity for consulting this work, but found a quotation made by Ayers from it, which contains the view referred to.

² "Beiträge zur Anat. and Phys. der Dipnoër," *Jenaische Zeit.*, Bd. xviii.

³ *Op. cit.*

cells similar to those of lymph being enclosed in the meshes thus formed. It would seem, from the descriptions of this and other authors, to be constant in presence and position, and it cannot therefore be one of those accidental infiltrations of the tissue with leucocytes which are so commonly found in every part of the intestine. It appears then that structures which may be correctly termed lymph follicles are to be found in the intestinal tracts of *Acipenser*, *Dipnoi*, and some *Selachians* only among fishes. Further research may, however, correct or extend this list.

In *Acipenser* the lymph follicles of the spiral valve are the representatives of the closed follicles forming the Peyer's patches in the higher vertebrates. They can usually be seen by the help of a magnifying hand-glass, as minute, whilst spots unequally distributed in the valve, which has, contrasted with them, a dull white colour. At some points they are so densely crowded together as to form an almost complete resemblance to a Peyer's patch.

The remaining part of the mucosa in the neighbourhood of the spiral valve in *Acipenser* and *Amia* is loaded with lymph corpuscles, although not nearly to the same extent as the follicles of the former.

END-GUT.

The relative lengths of this part of the intestine in *Acipenser* and *Amia* have been given above.

In some specimens of *Acipenser* there was practically no end-gut, the last turn of the spiral valve extending to the anal aperture. Where, however, it acquires any length, the mucosa covering it is either smooth or thrown into slender longitudinal folds, and is sometimes provided with minute crypts. The epithelium consists of cylinder and goblet cells, which gradually shorten to cubical cells, and at the vent to flattened cells, forming several layers in thickness. Anteriorly the cylinder cells bear a short fringe of cilia.

In *Amia* the inner surface of the end-gut is folded longitudinally; sometimes it is smooth and provided with crypts. When the epithelium is removed by maceration, the surface has a reticulated appearance. The epithelium consists of ciliated

cylinder cells with a few goblet cells. It undergoes a gradual decrease in height towards the vent.

In *Lepidosteus* the epithelium is of the character of that of the mid-gut, but the cilia are thicker and longer. At the vent the cells become cubical, which form gives no evidence of the possession of cilia.

I have observed in *Lepidosteus* the mesentery which connects the end-gut with the ventral wall of the peritoneal cavity, and which was discovered and described by Balfour and Parker.¹

THE PYLORIC APPENDAGE.

The pyloric appendage in *Acipenser* and *Lepidosteus* differs from similarly situated organs in other fishes, in that it is a compound structure with its pouches communicating with the intestinal cavity by a common duct, whereas in the great majority of fishes each pouch opens singly into the mid-gut. The latter arrangement is the primitive one; it can be seen in very young *Lepidostei*, in which the cæca arise as isolated out-growths of the intestinal wall, and assume later a common duct, this being the manner of development in the Sturgeon also, according to Balfour.²

In *Acipenser* the organ is flattened on its inferior face, and appears uniform. The duct opens on the left side of the mid-gut, about a centimetre from the pyloric valve. It is of such a dimension in very large Sturgeons as to permit readily the introduction of the index finger into it for some distance, but in Sturgeon of ordinary size it is of the diameter of a goose-quill. Ten to twenty cæca, arranged in a radiate fashion, open into it at a distance of a centimetre or so from its intestinal aperture, all the cæca being enclosed in a common sheath of muscular and connective tissue. The mucosa of the duct and cæca is arranged in folds, crypts, and tubules, in much the same way as it is in the mid-gut. When denuded of its epithelium it appears possessed of the same characteristic network of the subepithelial tissues.

In a thin vertical section of the appendage, placed under the microscope, the structure of the mucosa is seen to differ un-

¹ *Op. cit.*

² *Comparative Embryology*, vol. ii. p. 632.

essentially from that of the mid-gut. The epithelium possesses more nuclear layers, the cilia are shorter, the cylinder cells slightly larger, and the goblet cells more extended than in the intestine. The connective tissue between the tubules is very abundant, and at various points in it there are collections of leucocytes.

The two muscular layers of the mid-gut are extended over the duct and cæca of the organ, but on the latter are arranged obliquely with regard to each other.

In *Lepidosteus* the organ appears more lobed, and presents the shape of a bean in young forms, in which it extends over the inferior face of the gall bladder and pancreas for some distance. Its lobes or cæca are very numerous, the common duct into which they lead opening into the mid-gut immediately behind the pyloric valve. The epithelial lining of both duct and cæca is of exactly the same character as that of the mid-gut.

In *Amia* there is no pyloric appendage.

Various theories have been put forward as to the function of these organs. The earliest opinion, and one for a time generally adopted, was that they act collectively as a pancreas in the absence of the latter organ. Whatever support this view had was taken from it when it was shown that pyloric cæca and a pancreas may consist in some fishes, notably *Lota*.

In 1860, Mordecai¹ advanced the view that these organs collect and store up fluid nutritious matter, which, during the passage of the fish to its spawning ground, is absorbed and utilised to repair the wasting processes of the body in the absence of ordinary food. His observations were made on *Alosa præstabilis* (*Clupea sapidissima*, Wilson), in which there are from sixty to one hundred separate cæca, and these, during the ascent of a river by the fish, were found distended with a brownish mucus, which was absent at other times of the year. Mordecai found also that the number of the cæca increase with age, and that in *Labrax* and *Dioplites*, some rudimentary in younger forms are functional in the fully adult.

According to Edinger,² the cæca serve to suck up the liquid

¹ His pamphlet is republished in the *Bull. U.S. Fish Commission*, 1881, p. 227.

² *Op. cit.*

and digested food matter as it escapes from the stomach, and absorb it. Wiedersheim¹ also adopts this view, and tries to show that the development of the pyloric appendages stands in inverse relation to that of the spiral valve. He mentions two instances of this: *Polypterus*, in which the pyloric appendage is but a short cæcal pouch, while the spiral valve is highly developed, and *Lepidosteus*, which has a well-developed pyloric appendage, but no spiral valve. This view of Wiedersheim, it must be said, cannot be held as generally correct, even when applied to the Ganoid fishes alone, for in *Acipenser*, in which the cæca being provided with a common duct is an evidence of the great development of these organs, there is a well-marked spiral valve, and in *Amia*, in which the spiral valve is almost as rudimentary as in *Lepidosteus*, there are no pyloric cæca.

Krukenberg² found in the cæca of *Acipenser sturio* evidence of the presence of diastase, pepsin, and trypsin. In other fishes these organs gave extracts containing one or more of the same enzymes. Krukenberg is, however, inclined to believe, after a long series of experiments, that the pyloric appendages perform specially the function of absorption.

According to Stirling's³ view, these organs subserve different functions in different fishes, being absorptive in some, and in others glandular, secreting trypsin in some cases in important quantities.

Blanchard⁴ found that the extract of the pyloric cæca in various fishes effects the transformation of boiled starch into grape sugar, and that when boiled white of egg or fibrin is added to the extract, whether this is alkaline, acid, or neutral in its reaction, peptones are formed. He believes that a tryptic ferment alone is present to accomplish the latter result.

During the summer of last year, I made a number of experiments with extracts of the pyloric organ in *Acipenser*, in order to determine the presence of the enzymes, which Krukenberg affirms he found there. For this purpose large fish were employed. The organ after its removal was slit open, the mucous matter in the duct and cæca quickly washed away, to

¹ *Lehrbuch der Vergl. Anat.*, p. 585.

² Kühne's *Untersuchungen*, Bd. ii., 1882.

³ *Journal of Anat. and Phys.*, vol. xviii. p. 426.

⁴ *Comptes rendus*, xcvi. 1241-1244.

remove such enzymes as might have gained entrance from the intestine, and which would vitiate the result. It was then in some cases finely minced, and in this condition covered with distilled water in a flask surrounded by ice for twenty-four hours; in others it was carefully dried, and in a finely divided state extracted at a temperature of 35° C., with a 0.2 per cent. solution of hydrochloric acid, or with a 0.5 per cent. solution of sodic carbonate. With extracts made with distilled water, no conversion of starch into grape sugar could be obtained, and in no case could the presence of the latter substance be detected. Almost always an emulsion occurred when a quantity of the extract was shaken with some olive oil and allowed to stand. From the acid or alkaline extracts of the finely divided organ I was unable to obtain the slightest traces of digestion when fibrin or boiled white of egg was treated with them; if, however, the organ was slightly sponged, instead of being quickly washed with water, traces of pepsin and trypsin were found, but no diastase, although grape sugar could be detected in very slight quantities. The presence of trypsin can be easily explained in this case, as the opening of the pancreatic duct is just opposite that of the pyloric organ, and in the first contraction of the intestine after the pancreatic fluid escapes some of the fluid must find its way into the duct and cæca, even if it does not reach them by any other means, *e.g.*, diffusion. The pepsin gains access in like manner from the fluid contents of the stomach, immediately after passing through the pyloric orifice.

The difference between the results obtained by Krukenberg and those here detailed, as to the presence of enzymes in the pyloric appendage of *Acipenser*, may be accounted for on the ground that in all the material used by me the stomach and intestine were completely empty, while it is barely possible that it may have been otherwise with that employed by Krükenberg, since enzymes are more likely to be present in detectable quantities when food matter is in the intestinal canal.

Although it is an important matter to establish whether the enzymes referred to are present or not in the pyloric cæca, and in what quantities, yet such an accomplishment must not be allowed to decide definitely what the function of the organs is in the great majority of fishes. Pepsin and trypsin may be

normally present as a result of their easy diffusion, as is sometimes observed in organs not immediately connected with the alimentary canal in higher vertebrates, or they may be present as the result of the active secretion of the cæca. That such a secretion can occur and does, is possible, apart from the fact that in certain fishes, *e.g.*, in the cod, according to Stirling, the cæca are provided with gland structures of the usual form. It is true that the cæca are lined with cylinder cells usually, to which there has not yet been attributed the power of secreting either pepsin or trypsin. But when it is seen that the long cylinder cells lining the intestinal tract and the so-called liver in *Amphioxus* must secrete whatever enzymes are used in the digestion of the food swallowed, one is compelled to ask, Why should not a somewhat similar epithelium in the pyloric cæca of fishes perform a like function? The secretory function of this epithelium, as Stirling points out, does not exclude that of absorption, this also being exemplified in the case of *Amphioxus*. We see, therefore, that it is not easy to determine definitely the function of these organs in all fishes; in some, absorption may overshadow secretion, in others, the reverse may occur, while in others again, the two functions may occur in equal proportions. This would explain the contradictory results obtained by different observers in this field of research.

In any case, it is fair to conclude that the pyloric cæca are rudimentary structures once actively glandular. They are in their development remarkably similar to other outgrowths of the intestinal wall in their immediate neighbourhood, *i.e.*, the liver and pancreas. It seems extremely probable that at one time in the history of vertebrates there opened into the alimentary canal, which had a simpler form than it now possesses, a large number of pouch-like diverticula, and that by gradual specialisation of some of these arose posteriorly the liver and pancreas, anteriorly the air bladder, and, if they are not homologous with the latter, the lungs, while others retained their primitive structure and arrangement, persisting as pyloric cæca. In consequence of this specialisation, all the functions, such as those of absorption and of the secretion of enzymes, possessed by the original cæca, would necessarily be retained in an impaired degree by those persisting in that form.

It is to be expected, also, that the digesting principles secreted by the cæca partake more or less of the characters of those of the primitive organs. We may in this way explain the occurrence of such an enzyme as Blanchard found in the pyloric appendages, which digests in an alkaline, acid, or neutral solution; this, probably, was the character of the primitive secretion, not only of these organs, but of the whole intestinal tract, and by a course of selection operating in the organs and their functions the secretion came in the course of time to present in the stomach the properties of pepsin, in the pancreas those of trypsin. We have then a clue to an explanation of the supposed presence of both enzymes in the pyloric cæca; one enzyme in reality is present, which digests fibrin in an alkaline or an acid solution, and which partakes of the characters of both pepsin and trypsin.

THE PANCREAS.

It is over half a century since the first observation on the pancreas of fishes was published, and it is only twelve years ago that the presence of such an organ was demonstrated to be general in this class. To Legouis belongs the honour of having accomplished the latter task.

This observer¹ has given a full history of the researches of the various anatomists on the subject, and on this account further reference to the general literature bearing on it may be avoided. With regard, however, to that treating of the pancreas of Ganoid fishes a few words here are necessary.

In 1833 Alessandrini² discovered a pancreas in the Sturgeon. After a number of anatomists had failed to confirm this discovery, Leydig³ recognised the accuracy of Alessandrini's description, and, what the latter had not done, gave a short account of the histological structure of the organ.

Alessandrini's and Leydig's statements have not been confirmed by the researches of a third observer up to the present date. Wiedersheim⁴ describes as the pancreas an organ extending from

¹ *Ann. des Sciences Nat.*, 1873.

² *Ann. des Sciences Nat.*, t. xxix., 1833; also *Acad. Scien. Inst.*, Bonon, 1835, tom. ii.

³ *Untersuch. über Fische und Reptilien*, Berlin, 1853.

⁴ *Lehrbuch der Vergleich. Anat.*, p. 605.

the pyloric appendage down the left side of the anterior portion of the mid-gut, while Krukenberg¹ found no organ specially performing the function of a pancreas, and he maintains that the organ of Wiedersheim, which he regards as the spleen, is neutral as to digestion, its extracts having no action whatsoever. Ayers² has given a figure of a section of the supposed pancreas, and he recognises it as constituted of lymphoid tissue.

No reference has hitherto been made in the literature to the occurrence of a pancreas in *Amia*.

In *Lepidosteus* Balfour and Parker³ found a pancreas in young forms, it being situated, according to their description, behind the liver in the loop of the pyloric section of the stomach. They found also that it arises in the embryo in the same manner as in other vertebrates, and that late in larval life it envelops the anterior section of the bile-duct. In the fully adult *Lepidosteus* they observed a small, apparently glandular, mass connected with the bile-duct, and occupying a position similar to that of the pancreas in the larva. They were unable to decide on its nature, as its poor preservation did not permit a histological examination.

In *Acipenser*, the organ considered by Wiedersheim to be the pancreas is really the spleen, as a careful study of its histology will show.

The true pancreas in this fish is a disseminated one, *i.e.*, its tissue is not localised, but variously extended throughout the the right half of the peritoneal cavity. It occupies on the whole the position described by Alessandrini and Leydig. Its tubules and ductlets entwine about the branches of a blood-vessel (*arteria colliaco-mesenterica*), which it accompanies down the valvate portion of the intestine, on the median and anterior portions, and into the liver (fig. 16). It was in sections of the last-named organ that I found it first. It is more disseminated in some specimens of *Acipenser* than in others; for example, in one I found that it extended 8 cm. down the length of the valvate portion of the mid-gut, while usually the distance extended is only about 3 cm. The greater bulk of the organ is found

¹ Kühne's *Untersuchungen*, Bd. i. and ii.

² *Jenaische Zeitschrift.*, Bd. xviii. p. 479, taf. xvii. fig. 52.

³ *Phil. Trans.*, 1882, pt. i. p. 359.

between the liver and the second bend of the mid-gut on the right side, and is easily detectable from the thickness of the walls of the blood-vessel referred to, consequent on the pancreatic tissue enveloping them. As a branch of this artery enters the accessory spleen (fig. 16, *asp*), vertical sections of the latter organ sometimes betray the presence of the pancreatic tubules.

The serosa covering the pancreatic tissue and the vessels has usually a dark colour, sometimes perfectly black, owing to the presence of a large number of pigment cells.

The portions of the pancreas which are attached to the intestinal walls are always closely applied to the latter and included within the serosa.

The pancreatic duct opens into the mid-gut on the dorsal side; its aperture and that of the bile duct being found on a prominent papilla on the inner intestinal surface, not more than half a centimetre usually from the tip of the pyloric valve. I have never succeeded in injecting the pancreatic duct with coloured fluids so as to show its course. It is easily distinguishable from the bile duct by the greenish tinge which the latter always has.

In *Acipenser sturio* Alessandrini found the bile duct and the pancreatic duct to open on separate but similar papillæ on the inner wall of the mid-gut, that on which the opening of the pancreatic duct is found being placed more than 2 cm. from the pyloric valve. I cannot find this to be the case in *Acipenser rubicundus*, in which, by snipping off the point of the single papillæ above referred to and spraying the stump with water, one can easily see the two apertures placed side by side on it.

In *Amia* the pancreas is disseminated in a manner similar to what it is in *Acipenser*. A part of it is found adherent to the extreme anterior end of the mid-gut (fig. 10, *pn*), but a greater part envelops the larger branches of the portal vein in the interior of the liver. It forms a large portion of the bridge between the right and left hepatic lobes, and it covers, to a certain extent, the arch of the bile duct.

The pancreatic duct is here also hard to trace. I did this, however, in a young *Amia* of about 6 cm. in length, by means of a series of vertical sections made by Professor Ramsay Wright, who was the first to observe the presence of a pancreas in this fish. A careful dissection of the tissues about the bile duct in

the adult gave the same result as the study of the series of sections. The pancreatic duct is much narrower in diameter than the bile duct, to which it is nearly parallel, and near the intestinal wall they both have a common investment of connective tissue, the one thereby appearing to open into the other. They remain completely separate, and their apertures are to be found on the apex of a slender papilla placed about 1.5 cm. from the pyloric valve. The course of the two ducts is from before backward, almost in a line with the anterior part of the mid-gut.

In *Lepidosteus* the pancreas is not so widely disseminated as in either *Acipenser* or *Amia*. It envelops the portal vein as it runs along partially sunken in the dorsal face of the liver, in the posterior third of this organ, while it reaches behind accompanying the same vein to a point opposite the posterior extremity of the pyloric appendage (fig. 1, *P*). Some of its tubules are adjacent to the superior face of the gall bladder, others twining about the bile duct for some distance. In the liver the tubules radiate frequently out from the vicinity of the portal vein between the hepatic lobules. Both the bile duct and that of the pancreas run side by side backward to the mid-gut, the pancreatic duct being placed on the gastric side of the other. Adjacent to the wall of the mid-gut the two ducts become fused. In a transverse section of this part of the body it is possible to distinguish this common duct from a pyloric caecum only by tracing it from behind forwards, since the histological structure of both near their termination in the intestine are alike in every particular. Opposite the pyloric appendage, and above the pylorus, is a small quantity of lymphoid tissue, which, though it contains a few tubules of the pancreas, is not the latter organ, as Balfour and Parker suppose. This, usually as large in vertical section as the mid-gut, and, traversed by the portal vein, seems to be an accessory spleen, the pancreatic tissue forming but a very small part of it.

I have not had an opportunity of studying sections of the liver of an adult *Lepidosteus*, but I have no hesitation in saying that such sections, if taken through the posterior third of the organ, would show well-developed pancreatic tissue surrounding some of the larger vascular channels near the dorsal surface, and

that the pancreas in this fish is not inferior, structurally and functionally, to what it is in either *Acipenser* or *Amia*.

With regard to the finer histology of the pancreas in the three genera a short description only can be given here, as the quantity of material at my disposal did not allow very varied methods of preparation.

In *Acipenser* the structure is very much as in the higher vertebrates. In the necks of the tubules, which may also be termed the intermediary canals of the alveoli, the lining epithelium is constituted of cubical cells. In the alveolar portions the cells are large, the nuclei distinct and arranged in the peripheral halves of the cells, while the central halves are filled with granules. In my preparations the nucleus may be said to be the only part of the cell which stains in carmine or hematoxylin, as it is rare that the protoplasm in the immediate vicinity of the nucleus takes any tint at all. The alveolar lumen is usually distinct and of a zigzag course. Transverse sections of the tubule in its various parts exhibit the usual characteristic appearances.

Among the cells and in the lumen of each alveolus, there are other cellular elements, which are noticeable at first sight on account of the deep and nearly uniform staining which they take, and also on account of their varied shape, sometimes oval or polyhedral, and sometimes amoeboid. Granules are lacking, the protoplasm appears clear, and no reticulation was observable in it. The nuclei always stain much more deeply than those of the ordinary cells of the alveoli. The cells are oftenest to be found in the lumen, and then they appear sometimes to send out processes between the gland cells (fig. 17, C.). They are, I think, remarkably similar to the centro-acinar cells of Langerhans. I have never met with these structures in any other fish.

The arrangement of the tubules about a branch of the *arteria coeliaco-mesenterica* is indicated in fig. 17, A. Trabeculae of connective tissue radiate outward between the tubules to the serosa, the latter possessing a large number of pigment cells, to which the dark colour commonly associated with the pancreas in this fish is due.

In *Amia* the pancreatic tubules imbedded in the liver are twined about the larger branches of the interlobular veins in the

manner represented in fig. 18. The connective tissue of the interlobular septa run between and separate the neighbouring tubules, which in a vertical section of the liver appear cut in various directions, oftener longitudinally. The cells of the aveoli are, in their central portions at least, crowded with granules, and stain very feebly apart from their nuclei. Near the lumen the limits of the cells are indistinct, owing to the quantity of granules present. The lumen sometimes is, and sometimes is not, visible.

In *Lepidosteus* an alveolar and an intermediary portion can be distinguished in each pancreatic tubule.

The pancreas would appear to be rudimentary or absent in but very few fishes. There are conditions when such an organ seems to be useless, and these are found in small fishes only, such as some of the Cyprinoids, in which digestion by the stomach alone prepares enough of nutritious material for absorption to satisfy the demands of the organism, and in which the mid-gut does not serve to submit the food matters escaping from the gastric cavity to a second digestive process but to a further absorption. No such reason can be advanced for the supposed absence of the pancreas in large fishes. Its presence is so disguised in many forms that one finds it impossible to decide definitely whether it is absent in others. In Ganoids, as above described, it is partially imbedded in the liver, in some Siluroids¹ completely so. Why may it not be connected in a like manner with the liver in other forms in which it is now supposed to be absent? That this is frequently the case is probable from the occurrence of trypsin in the extracts of the liver of various fishes, as shown by Krukenberg. The liver and pancreas thus fused into one organ can of course in no case be considered as a hepato-pancreas.

¹ In *Amiurus* the pancreas is imbedded in the interior of the liver, its tubules being entwined about the interlobular veins, (see *Proceedings Canad. Inst.*, Toronto, new series, vol. ii. No. 3).

EXPLANATION OF PLATE XX.

Fig 1. The alimentary canal and pancreas of *Lepidosteus*, from a specimen measuring 10 cm. *a*, œsophagus; *b*, the commencement of the stomach anteriorly; *c*, the pylorus; *e*, the anterior or duodenal section of the mid-gut; *f*, the posterior, or valvate, section of the same; *at*, the hind-gut; *ap*, the pyloric appendage; *p*, the pancreas. (Reduced.)

Fig. 2. A longitudinal section of one of the papillæ of the so-called œsophagus in *Acipenser*.

Fig. 3. An oblique section of a dilated sac from the œsophagus of *Acipenser*.

Fig. 4. A transverse section of a dilated sac from the œsophagus of *Amia*.

Fig. 5. A tubule from the mouth of the air-duct in *Amia*.

Fig. 6. A vertical section of a fold of the mucosa of the œsophagus of *Lepidosteus*, showing ciliated epithelium and dilated sacs.

Fig. 7. Two glands from near the posterior part of the cardia in *Acipenser*.

Fig. 8. A gland from the cardia of *Amia*. *a*, one seen in transverse view.

Fig. 9. Part of a mucous gland from the pylorus of *Acipenser*.

Fig. 10. A vertical section of the wall of the anterior part of the mid-gut in *Amia*. *pn*, the pancreas; *m*, the mucosa; *i*, the inner, *o*, the outer, muscular layer.

Fig. 11. Epithelium of a crypt of the mid-gut in *Acipenser*.

Fig. 12. Part of a vertical section of the spiral valve in *Acipenser*, showing the short pouches of the epithelium, and the mucosa underneath richly laden with lymph corpuscles.

Fig 13. Epithelium of the same section more highly magnified. *a*, a young epithelial cell.

Fig. 14. A section of a lymph follicle from the spiral valve of *Acipenser*; the greater number of lymph corpuscles have been removed from the section by agitating it in water.

Fig. 15. Epithelium of a tubule of the spiral valve of *Amia*.

Fig. 16. A view of the mid-gut and the organs attached to it in *Acipenser*. *Ap*, the pyloric appendage; *sp*, the spleen; *a.sp*, the accessory spleen; *p*, the main portion of the pancreas surrounding a branch of the *arteria coeliaco-mesenterica*; *p'*, *p''*, pancreatic tissue adhering to the smaller branches of this vessel, and to the wall of the mid-gut; *l*, the liver, the course of the pancreatic tissue in which is represented by dotted lines; *m*, the anterior portion of the mid-gut; *v*, the valvate portion of the same.

Fig. 17. *A*, A section of a branch of the *A. coeliaco-mesenterica* in *Acipenser*, with pancreatic tubules surrounding it, a portion only of these being represented; *B*, a part of one of the tubules more highly magnified; *C*, a transverse view of one of the tubules. In both *B* and *C* the centro-acinar cells have a darker shading. *B* and *C* highly magnified.

Fig. 18. From a vertical section of the liver in *Amia*, showing the manner in which the pancreatic tubules are arranged around a larger interlobular vein; *pt'*, one of the tubules seen in transverse section; *vt*, an interlobular vein filled with blood-corpuscles.

Fig. 19. From a vertical section of the dorsal face of the posterior part of the liver in *Lepidosteus*, showing the arrangement of the pancreatic tubules *pt* about the portal vein (*vp*); *h*, liver tissue; *b*, the bile duct.

THE NEURAL SPINES OF THE CERVICAL VERTEBRÆ
AS A RACE-CHARACTER. By D. J. CUNNINGHAM,
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University of Dublin.*

SIR RICHARD OWEN,¹ in one of the numerous important articles which he has contributed upon the Anatomy of the Anthropoid Apes, has compared the vertebral column of the Gorilla, Orang, and Chimpanzee with that of several of the different races of man. In this he remarks that "in the skeleton of a Boschisman, as well as in that of the female Australian in the Museum of the Royal College of Surgeons, the spines of the five lower cervical vertebræ are simple." He further observes that the neural spines of the 3rd cervical vertebra in a male Australian is "not bifurcated as usually in Europeans."

Before my attention was drawn to these observations of Sir Richard Owen, I had collected statistics regarding the condition of the neural spines of the cervical vertebræ in a number of the lower races of man, and, as these extend considerably the data recorded on this subject, I have thought that their publication might not be without some interest. It will generally be noticed that in low races the cervical neural spines are relatively shorter and more stunted than in the European. More especially can this be observed in the case of the neural spine of the 3rd cervical vertebra. This condition is obviously for the purpose of allowing a greater freedom of movement in the cervical section of the spine, and is to be associated with other peculiarities present in the lumbar region of the low races which give to the loin segment a greater flexibility and suppleness.² But the feature which especially attracts attention is the condition of the extremities of the cervical neural spines. As Owen has pointed out in the case of the Australian and Bushman, the cervical spines in the low races are as a rule non-bifid or only very slightly so.

¹ "Comparison of the Lower Jaw and Vertebral Column of the *Troglodytes gorilla*, *Troglodytes niger*, and *Pithecius satyrus* and Different Varieties of the Human Race," *Trans. Zool. Soc.*, 1851, vol. iv.

² *Vide Nature*, Feb. 16, 1886, "The Lumbar Curve," by D. J. Cunningham.

With the view of determining the comparative frequency of this character in the different races of man, I have examined the spines of 15 Europeans, 7 Australians, 6 Negroes, 4 Andamans, 3 Tasmanians, 1 Bushman, and 2 Esquimaux, and in recording the results which I have obtained I must give expression to my sense of the deep obligations under which I lie to Dr J. G. Garson of the Royal College of Surgeons in England, and to Professor Macalister of Cambridge. The number of spines of the low races in the Trinity College Museum were too few in number to allow of me carrying out this investigation in Dublin, and I had necessarily to ask the permission of these gentlemen to examine the specimens under their charge. This was accorded to me in the freest manner possible.

The spine of the 7th cervical vertebra is never bifid, and that of the 6th is rarely cleft even in the European. In the following tables, therefore, the condition of the spines of the 2nd 3rd, 4th, and 5th cervical vertebræ is alone recorded. It will be observed that the spines are arranged in three groups—(1) the first comprises those which are distinctly bifid; (2) the second includes those in which there is merely an indication of bifidity; and (3) the third those which show no trace of it whatever.

Condition of Neural Spines of Cervical Vertebrae in Fifteen Europeans.

	Bifid.	Feebly Bifid.	Non-Bifid.
2nd cervical vertebra, . . .	15
3rd cervical vertebra, . . .	10	3	2
4th cervical vertebra, . . .	9	4	2
5th cervical vertebra, . . .	9	5	1

Condition of Neural Spines of Cervical Vertebrae in Seven Australians.

	Bifid.	Feebly Bifid.	Non-Bifid.
2nd cervical vertebra, . . .	7
3rd cervical vertebra, . . .	2	...	5
4th cervical vertebra, . . .	1	2	4
5th cervical vertebra, . . .	2	2	3

Condition of Neural Spines of Cervical Vertebrae in Three Tasmanians.

	Bifid.	Feebly Bifid.	Non-Bifid.
2nd cervical vertebra, . . .	3
3rd cervical vertebra,	1	2
4th cervical vertebra,	1	2
5th cervical vertebra,	1	2

Condition of Neural Spines of Cervical Vertebrae in Six Negroes.

	Bifid.	Feebly Bifid.	Non-Bifid.
2nd cervical vertebra, . . .	2	3	1
3rd cervical vertebra, . . .	1	2	3
4th cervical vertebra, . . .	1	1	4
5th cervical vertebra, . . .	1	2	3

Condition of Neural Spines of Cervical Vertebrae in Four Andamans.

	Bifid.	Feebly Bifid.	Non-Bifid.
2nd cervical vertebra, . . .	3	1	...
3rd cervical vertebra,	2	2
4th cervical vertebra,	2	2
5th cervical vertebra,	2	2

In one Bushman the neural spine of the 2nd cervical vertebra was bifid; that of the 5th feebly bifid, and those of the 3rd and 4th non-bifid. In two Esquimaux the neural spines were feebly bifid throughout in one specimen, whilst in the other the only neural spine which was bifid was that of the 2nd vertebra; those of the remainder were non-bifid.

The following table gives the combined results of the 24 low races that have been examined:—

Condition of Neural Spines of Cervical Vertebrae in Twenty-four of the Low Races of Man.

	Bifid.	Feebly Bifid.	Non-Bifid.
2nd cervical vertebra, . . .	18	5	1
3rd cervical vertebra, . . .	3	6	15
4th cervical vertebra, . . .	2	7	15
5th cervical vertebra, . . .	3	10	11

By comparing the results given in this table with those which are recorded for the Europeans, a very marked difference in the condition of the neural spines will be observed. The only cervical vertebra which presents an invariably bifid neural spine in all the races is the axis vertebra. In only one instance, viz., in a Negro, have I found it non-bifid. This character, however, is shared by the Chimpanzee, and also in some cases a trace of the same bifidity may be noticeable in the corresponding neural spine of the Gibbon, and likewise even in the Orang and Gorilla.

In the Europeans the neural spines of the 3rd, 4th, and 5th cervical vertebræ are as a rule bifid. In only one case did I find all these spines non-bifid in the same individual.

In the low races, however, the reverse condition is the rule, and in this respect they resemble the corresponding neural spines of the Chimpanzee. They differ from the latter, however, in being more stunted and not so sharp at the point.

It will be observed from the tables that have been given that the two neural spines in the low races which are least frequently bifid are the 3rd and 4th. These also are the most stunted of the series. By this arrangement the longer spines above and below are allowed to close over them in extension of the neck.

[*Editorial Note.*—As additional references, we may say that M. Hamy, in his excellent description of the skeleton of an Aëta Negrito woman (*Nouv. Archives du Museum*, 1879, vol. ii.), has also directed attention to the tendency in the coloured races for the cervical spines, the axis excepted, to be non-bifid, and a number of examples have also been recorded by the writer of this note in his "Challenger" Report on the Bones of the Human Skeleton, part ii., now in type, and shortly to be published. W. T.]

VARIATIONS IN THE NERVE SUPPLY OF THE
FLEXOR BREVIS POLLICIS MUSCLE. By H. ST
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ONE of the earliest facts impressed upon the student, when he takes up the study of Practical Anatomy, is the relatively slight tendency shown by nerves to vary; in particular, the nervous supply of muscles is supposed to be immutable. This dogma has been extended to Comparative Anatomy by the Heidelberg School, and Professor Ruge "asserts, with Gegenbaur, that a muscle is to be regarded as the end-organ of a nerve, and therefore when a muscle alters in position and connections, its original and typical relations can always be identified by its nerve of supply."¹

In the foot, where in man the muscles are arranged upon a more primitive plan than in the hand, we find that the abductor and flexor brevis pollicis are supplied by the internal plantar nerve, while all the other intrinsic muscles receive their supply from the external plantar. It is interesting to note the deviation from this fundamental arrangement among the Mammalia as worked out by Professor Cunningham. He says:—

"In the Elephant the internal plantar nerve supplies the flexor brevis indicis; in the Hyrax the internal plantar nerve supplies the flexor brevis indicis, the adductor indicis, and the second dorsal interosseous muscle; in the Beaver a still more remarkable deviation is found. From the internal plantar nerve proceed the twigs of supply for the abductor hallucis, flexor brevis indicis, flexor brevis medii, and the first and third dorsal interossei. Lastly, in the Fox-bat there is an example of the external plantar nerve encroaching on the domain of the internal plantar, by supplying a twig to the outer head of the flexor brevis hallucis."²

This is a most interesting case of two nerves struggling, as it

¹ *Morphologisches Jahrbuch.*, 1878,—quoted by Professor Cunningham. *Challenger Reports*, part xvi. p. 49.

² *Op. cit.*, p. 135.

were, for a group of muscles, sometimes the internal plantar gaining ground, at other times the external plantar extending its domain.

In this paper I have to record a similar struggle (if we may call it so) between the two homologous nerves of the human hand, the median and the ulnar; and we shall find that the nerve-supply to muscles is not immutable, even when our observations are confined to one animal—Man.

*Table of Variations in the Nerve-Supply of Flexor Brevis
Pollicis in Man.*

Outer head supplied by deep branch of ulnar alone, . . .	5 cases.
Outer head supplied by ulnar and median, . . .	19 „
Outer head by median, inner head by ulnar, . . .	5 „
Median giving twigs to both heads; inner head also with an ulnar nerve-supply, . . .	2 „

In some of these cases the twig from the deep branch of the ulnar nerve to the outer head was large; in others very small. The size of the twigs from the median was in inverse proportion to those from the ulnar.

We are told in the text-books, Continental as well as English, that the outer head of flexor brevis pollicis is supplied by the median nerve, and the inner head by the deep branch of the ulnar. This seems at first sight a deviation from the fundamental plan as observed in the foot, until we remember that Bischoff¹ has shown that the muscle usually described as inner head of flexor brevis is in reality a part of the adductor, the true inner head lying concealed beneath it on the metacarpal bone of the thumb, and described by Henle as the interosseus primus volaris. I have not as yet been able to trace the nervous supply of this true deep head of the flexor brevis, but in the two cases in my table, in which the median gave twigs to the inner head, I believe some filaments passed through it to reach the interosseus primus volaris.

It may be well to note that the outer head of flexor brevis usually consists of two parts; a large mass of fibres from the annular ligament and os trapezium (this is the true outer head), and a fasciculus from the inner head, which crosses the deep surface of the long flexor tendon to join the more superficial

¹ *Beiträge zur Anatomie des Hylobates leuciscus*, 1870, p. 20.

part at its insertion; it is the latter portion that one would naturally expect to receive an ulnar nerve-supply, but in every case both parts of the outer head received twigs. In the seven cases in which the outer head was supplied by the median alone, I found that in one case the contribution from the deep head was absent, in another it was very small; in the remaining five this point was not noted. I found it absent in both hands of a young female Chimpanzee, which was kindly placed at my disposal by Professor Cunningham; the outer head was here supplied by median alone. I am inclined to think that the fasciculus of fibres from the deep to the superficial head has acted as a bridge, and, as it were, dragged the branch of the ulnar nerve across. In one of the cases given in the above table the ulnar had encroached in a very unusual manner on the domain of the median; after giving twigs to the outer head of flexor brevis, it pierced the latter and supplied the opponens and abductor pollicis. The branches to the two latter muscles were as large as those which they normally receive from the median, and appear to have replaced the latter entirely.¹

At first sight it appeared as if this trespassing of the ulnar nerve on median territory might be explained by a communication between the median and ulnar in the arm, but in both arms of the Chimpanzee there was a very large communicating branch from the median to the ulnar in the fore-arm, and yet the outer head of flexor brevis was supplied by the median only.

As the distribution of the ulnar nerve described above has apparently escaped the notice of anatomists, a few words on the method of exposing it may not be out of place. The nerve in question usually comes through the adductor pollicis near its radial margin, and, passing on the deep surface of the long flexor tendon, pierces the outer head of flexor brevis. Sometimes it is entirely concealed by the adductor, and may be brought into view by separating the heads of the flexor brevis. It is surrounded by parallel strands of connective tissue, which give it an intensely deceptive appearance. In looking for this nerve I begin by securing the branches of the median to the outer head; these I find sometimes close to the annular ligament in company

¹ I had the pleasure of showing this rare case to Professor Cunningham, and also to the University anatomist, Dr T. E. Little.

with the nerves to abductor and opponens, often lower down from the first or second digital branches, sometimes in both these situations. I then rip up the sheath of the long flexor tendon, pull the latter aside, and separating the two heads of flexor brevis, by pushing without cutting, I see something stretching across which looks like a strand of connective tissue. I follow this into the muscle, and its nervous character becomes evident. I then take a note of the name of the student who is dissecting the part, and when he is doing the deep dissection of the palm he invites me to trace the nerve, and I verify its connection with the ulnar.

The first example of this nerve I found last winter session (1884-85), while dissecting a hand in the Dissecting Rooms of Trinity College, Dublin, and, supposing it to be a very rare anomaly, I showed it to Professor Cunningham. I found that he had an entry of a similar case in his note-book, and also the record of the dissection of the hand of a negro from Sierra Leone, in which the median gave twigs to both heads of flexor brevis. I must take this opportunity to express my thanks to Professor Cunningham for placing these two cases at my disposal.

In the five cases given in my table in which the radial head is said to be supplied by ulnar *alone*, the branch from the ulnar to the outer head was large; in two out of the five the whole dissection was made by myself, and after a very careful search I could not find any twigs from the median to the outer head. In the other three cases the integument had been removed before I examined the subject.

As in 19 out of 31 cases the outer head of flexor brevis had a double nerve-supply,¹ I think we should be justified in regarding this as the normal arrangement.

¹ From ulnar and median.

ON THE MORPHOLOGY OF THE INTRINSIC MUSCLES
OF THE LITTLE FINGER, WITH SOME OBSERVA-
TIONS ON THE ULNAR HEAD OF THE SHORT
FLEXOR OF THE THUMB. By H. ST JOHN BROOKS,
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University of Dublin.* (PLATE XXI.)

THE intrinsic muscles of the hand, more especially the marginal groups known in Human Anatomy as the "thenar and hypothenar eminences," have been frequently made the subject of investigation, but more from a descriptive point of view than with the object of elucidating their morphological value. In works on Human Anatomy great differences of opinion have prevailed as to the division and even the number of the short thumb muscles. Henle describes a double-headed flexor brevis distinct from the interosseus primus volaris, and also separate from the "outer head of flexor brevis" as ordinarily described in English text-books. The latter he terms a deep part of the abductor. Gegenbaur, on the other hand, ignores the presence of an ulnar or deep head altogether. Bischoff,¹ first threw light on the true ulnar head of flexor brevis pollicis, which he shows to be identical with the interosseus primus volaris of Henle, but he does not appear to think that the muscles of the little finger call for any special attention. Professor Young,² of the Owens College, Manchester, has contributed some valuable papers on the muscles of the hand, and adopts (provisionally) the classification first proposed by Professor D. J. Cunningham,³ of dividing the muscles of the manus and pes into three layers—

1. A plantar layer of "*adductores*."
2. An intermediate layer of "*flexores breves*."
3. A dorsal layer of "*abductores*."

Professor Cunningham has established this classification for the foot, and has shown that the organs of the marginal members

¹ *Beiträge zur Anatomie des Hylobates leuciscus*, 1870.

² *Jour. of Anat. and Phys.*, vols. xiv. and xvi.

³ *Zoology of the Challenger*, part xvi. pp. 19 and 48.

have a tendency to wander towards the heel. The abductores hallucis and minimi digiti are thus the marginal and enlarged "dorsal interossei." One of the most potent arguments by which Cunningham has established this theory is the fact, that in tetradactylous animals the origin of the (now marginal) abductor indicis is found farther back than the other interossei, unless confined by a rudimentary metatarsal. He adopts, with some reservation, the statement of Ruge,¹ that all the muscles which lie superficial to the deep division of the external plantar nerve are "contrahentes" or "adductores." But, he remarks, "the great objection to this method of classifying the adductors, however, is that it is incapable of being extended to the hand. In the manus the deep division of the ulnar nerve passes inwards, under cover of the flexor brevis minimi digiti and also under (or through) the opponens minimi digiti, both of which therefore, according to this generalisation, would be looked upon as contrahentes or adductores."²

The author believes that the facts detailed in this paper will show that this "flexor brevis minimi digiti" and the part of the opponens superficial to the deep ulnar nerve are really adductores. The true ulnar head of flexor brevis quinti in man is represented by that part of the opponens which lies beneath the deep ulnar nerve, and the radial head by the "third palmar interosseous." Further, the dissections described will tend to show that the true deep head of flexor brevis pollicis is very frequently indistinguishable; it is difficult to say whether it is suppressed, or fused with the adductor obliquus, the valuable guide of nerve relation being absent on the radial side of the hand.

With a view to establishing these points, I have examined the manus in Man, Chimpanzee (*Troglodytes*) Orang (*Pithecus*), *Cynocephalus anubis*, *Macacus nemestrinus*, *Colobus*, Marmoset (*Hapale*), Cat (*Felis domestica*), Capybara (*Hydrochaerus*), Virginian Opossum (*Didelphys virginiana*) and Australian Opossum (*Phalangista vulpina*). These animals were all most kindly placed at my disposal by Professor Cunningham from the stores of the Anatomical Department of Trinity College, Dublin.

¹ *Morph. Jahrbuch*, bd. iv. p. 645.

² *Op. cit.*, p. 136.

As I have to trace the wandering, both in origin and insertion, of the adductor or contrahentic¹ group of muscles, it will be well to mention what appears to be their typical condition. They are a group of flattened muscles, springing from a common pointed tendinous origin from the ligaments on the palmar aspect of the carpo-metacarpal articulation of the middle digit, and separated from the subjacent interossei by the deep branch of the ulnar nerve.² They diverge to be inserted into the proximal phalanges in such a manner as to adduct the fingers to a line which usually passes through the middle digit. The origins of the two marginal members (a^1, a^5 , fig. 2) show a great tendency to wander distally and thus overlie and dwarf the others; not only this, but they also spread towards the sides of the carpus, *creeping along the concavity of a curved plane*, formed partly by the unciform and os trapezium and partly by the anterior annular ligament. The insertion may also vary. Cunningham figures and describes a slip to the *radial* side of index finger in the hand of Cuscus, also a slip to the *fibular* side of the fourth digit in the foot of the Koala.³ Ruge⁴ describes and figures an adductor or contrahens passing to the *fibular* side of the fifth digit in the foot of *Dasyurus hallucatus*, while Cunningham figures a similar muscle in *D. viverrinus*, but describes it as "one of the abductors of the minimus," regarding the nerve relation as exceptional.⁵

In estimating what is a typical condition of adductores or contrahentes it appears to me that we should regard symmetry in size and direction of fibres rather than the presence of the full complement of muscles; the same remark applies to the flexores breves. The Cat affords a favourable example. It possesses two adductors for the index and little fingers, arising

¹ First described in the foot of Macacus by Halford of Melbourne, and named by him "contrahentes digitorum." He states that they are absent in the hand of the same animal (p. 12). In both of the specimens I dissected the contrahentes were well represented. "Not like man, bimanous and biped, nor yet quadrumanous, but cheiropodous." Melbourne, 1863.

² Ruge (*op. cit.*) established this nerve relation for the contrahentes of the foot, and it is evidently applicable to the hand also.

³ *Zoology of the Challenger*, part xvi., plate ii. fig. 3, *a*, and plate vii. fig. 2.

⁴ *Op. cit.*, p. 647.

⁵ *Op. cit.*, pp. 55 and 136; and plate xi. fig. 5, *d*^o. As far as I can judge from the figure the origin is close to the other adductors.

from the ligamentous structures of the central part of the carpus, and lying superficial to the deep ulnar nerve (fig. 1, a^2 , a^5). There are four paired flexores breves for the four ulnar digits. These are equal in size, and each arises near the base of the corresponding metacarpal by a pointed origin, which soon bifurcates into two symmetrical fleshy bellies, to be inserted into the ulnar and radial sesamoids. These all lie beneath the deep ulnar nerve. There are two short thumb muscles, one (f^1) representing the radial head or flexor brevis and the other (a^1) probably the adductor pollicis or first contrahens, as its origin is associated with the other adductores. If this view be correct, there is no trace of the ulnar head of flexor brevis. There is an abductor minimi digiti, but the muscle known in Human Anatomy as "flexor brevis minimi digiti"¹ is entirely absent.

In the Marmoset a very similar condition of the flexores breves is found, but we have here a different arrangement of the true flexor brevis minimi digiti (f); while the radial head (f^{br}) is inserted into the sesamoid as before, the ulnar head (f^{bu}) has no insertion into the phalanx either direct or indirect, but is inserted into the whole length of the metacarpal bone, forming an opponens. There is a "flexor brevis" minimi digiti (a^5a) arising from the hook of the unciform and from the anterior annular ligament and inserted with the abductor. It is relatively larger than in Man, and is separated by a small interval from the adductor quinti digiti; the latter and the adductor pollicis have spread in both directions in the manner indicated above. They thus unite in a median raphe as far as the metacarpo-phalangeal joint, and conceal the other two adductors (a^4 and a^2); they also travel along the curved plane towards the little finger and thumb respectively. An abductor pollicis and a radial head of flexor brevis pollicis are also present, but the ulnar head of the latter is either suppressed or fused with the adductor.

In Capybara we have chiefly to notice a remarkable case of suppression, while there are three powerful double-bellied

¹ As this name is confusing on account of the existence of a true flexor brevis of the little finger, I shall distinguish the "flexor brevis" of Human Anatomy by inverted commas, and by the letters a^5a (adductor quinti aberrans). The true flexor brevis minimi digiti is indicated by the letters f^{br} —radial head and f^{bu} —ulnar head.

flexores breves for the index, middle, and ring fingers, and the ulnar head of flexor brevis minimi (f^{bu}), is well represented, the radial head (f^{br}) is not merely entirely wanting, but its place is not taken by any other muscle. The two adductors (to index and minimus) have the typical arrangement, and the adductor minimi remains comparatively remote from the vacant space where the radial belly of flexor brevis ought to be. We shall compare this with the Opossum later on. There is an abductor, but no sign of "flexor bevis" minimi digiti (a^5a). The abductor indicis shows, in a marked degree, the tendency of marginal muscles to take their origin from a point more proximal than the rest of the group (the thumb being absent).

In the Virginian Opossum there exists a very remarkable condition of the adductor quinti digiti. A large triangular sheet of muscle, like that in the Marmoset, is present, but this extends further ulnarwards and arises from the median raphe and the ligamentous structures at the base of the metacarpus (fig. 2, a^5). This origin is continuous with another muscular mass arising from the base of the hook of the unciform (a^5a'), and diverging to be inserted into the ulnar sesamoid of the fifth finger. No sign of separation can be seen between these two muscles for at least a quarter of their length. Another muscle (a^5a) lies quite parallel to the one last described, and arises from the tip of the unciform hook and from the annular ligament; it is separated by a slight areolar interval from a^5a' , but the origins and insertions of the two muscles are absolutely adjacent and their fibres are perfectly parallel. The muscle (a^5a) is evidently the "flexor brevis" of Human Anatomy, as the origin, insertion, nerve-supply, and nerve relation are the same. There is a well-formed and typical abductor minimi having the same connections as in Man (fig. 2, abd^5), and there is also a muscle arising from the annular ligament near the origin of a^5a and running parallel to the radial side of the latter to give the perforated tendon to the fifth digit,—this is a flexor brevis digitorum manus. The broad adductor pollicis extends its origin radial-wards along the curved plane, and has concealed and coalesced with, or suppressed, the true ulnar head of flexor brevis pollicis. On removing the muscles which *lie superficial*

to the deep branch of the ulnar nerve a complete set of flexores breves come into view (fig. 3). On two of these, however, doubt may be thrown,—(1) the ulnar head of flexor brevis pollicis is probably only an artificially separated part of the adductor; (2) the minute radial head of flexor brevis minimi is partially blended with the fourth dorsal interosseous, and the existence of an arched tendon from the latter, “attached by one extremity to the distal end of the fifth metacarpal bone and by the other to the adjoining side of the first phalanx of the ring finger,” as described by Professor Young,¹ renders the discrimination more difficult. In both hands, however, dissecting from both palmar and dorsal aspect, I was able to trace a small fasciculus to the radial sesamoid of the fifth finger.² The ulnar belly (f^{5u}), a very small but perfectly distinct muscle, arises chiefly from the unciform but partly from the base of the fifth metacarpal, and is inserted into the ulnar sesamoid of the fifth finger. Both heads of the flexor brevis minimi are easily and naturally separable from a^5 and a^5a' , even without the aid of the deep ulnar nerve, which passes between them and makes “assurance doubly sure.”

Professor Young has arrived at results somewhat different from the above.³ He describes the abductor minimi (fig. 2, abd^5) as an opponens. (It arises from the pisiform bone, and is inserted into the ulnar side of the base of the proximal phalanx of the little finger. I could not find any fibres inserted into the metacarpal bone.) The muscle a^5a he calls the abductor, and a^5a' the ulnar head of flexor brevis; he has also a separation,⁴ of which I could find no trace, in the adductor minimi, marking off the ulnar margin of it as the radial belly of the flexor brevis.

It will be instructive at this stage to compare the foot of the same animal (fig. 4). Here we have an “annular ligament” presenting a superficial resemblance to the anterior annular ligament of the hand, though its connections are very different; but it has this property in common, that it affords a *curved*

¹ *Journal of Anat. and Phys.*, vol. xiv. p. 153.

² It will be remembered that in Capybara this muscle f^{5r} was entirely absent, though there could not be any fusion with another muscle in that case.

³ *Op. cit.*

⁴ *Op. cit.*, plate vii. fig. 1; a line between adm and f^5 .

plane along which the origin of a muscle can creep; and we have here a muscle (a^6a) whose insertion and nerve relation is identical¹ with the muscle similarly lettered in the hand, and whose general position appears very similar. Between this and the adductor quinti (a^5), we have an interval in which the deep branch of the external plantar nerve appears lying superficial to a well-developed double-bellied flexor brevis quinti. We note the complete absence of anything corresponding to a^5a' (fig. 2), also the slighter lateral extension of the origin of the adductor, quinti, therefore the lesser degree of functional replacement of and therefore the better development of flexor brevis minimi digiti. In the foot, unlike the hand, the fibular belly of flexor brevis hallucis (f^1f) is quite distinct, and arises in common with the tibial head considerably proximal to the adductor. I found an indication (not shown in the figure) of the separation into adductor obliquus and a. transversus described by Ruge² in *Didelphys cancrivora*. Ruge, however, gives no fibular head of flexor brevis hallucis for this species, and also omits all mention of the muscle a^5a which is present in *D. virginiana*; the latter muscle is figured and described (after Young) by Cunningham,³ but he calls it an additional head of the abductor, and the nerve relation is not shown or described.

The Australian Opossum or Vulpine Phalanger, while corresponding in a general way with the Virginian Opossum, shows some instructive differences. The adductor indicis is on the same plane as the adductor pollicis, so that adductores pollicis and indicis arise from the radial side of the central raphe and adductor minimi from its ulnar side. The muscles a^5a and a^5a' , which are separate in the Virginian Opossum (fig. 2), are here united to form one muscle, the deeper fibres of which (corresponding to a^5a') are inserted into the metacarpal bone, and are therefore homologous to a^5op (fig. 5 and fig. 8). The muscles corresponding to a^5a' and a^5 in the Virginian Opossum, although

¹ Besides the phalangeal insertion a strong fasciculus passes to the base, and a weaker set of fibres to the head, of the metatarsal bone. This reminds us of the development of an opponens from the corresponding muscle in the hand, so frequently found in higher forms, and is also an argument against regarding this muscle as a flexor brevis digitorum.

² *Op. cit.*, p. 648, and Taf. xxxv. fig. 49.

³ *Op. cit.*, p. 68, and plate vii. fig. 4, a^5a .

still united at their origin, are more distinct than in the latter animal, as there is a trace of an aponeurotic septum between them. The flexor brevis digitorum manus is absent, as the flexor sublimis supplies a perforated tendon to the fifth finger (while in Virginian Opossum the flexor sublimis has only three tendons, to the index, middle, and ring digits). On reflecting the layer of adductores, the deep branch of ulnar nerve is seen lying on the flexores breves. The fourth dorsal interosseous muscle shows the arched tendon to head of metacarpal and proximal phalanx of ring finger, as described by Cunningham in Cuscus, &c., and by Young in Virginian Opossum, but on the palmar surface of the latter muscle there is a beautifully distinct, fusiform, fleshy slip, inserted by a minute tendon into the radial sesamoid of the little finger; this is the radial belly of the true flexor brevis (*f^{br}*). The ulnar belly of the same muscle appears to be absent, while in the Virginian Opossum it is well represented (fig. 3, *f^{bu}*). The radial border of the adductor pollicis functionally replaces the ulnar head of flexor brevis pollicis; while arising in common with the well-developed outer head of flexor brevis, and inserted into the ulnar sesamoid of the thumb, is a distinct fibrous band, which is evidently the rudiment of the true ulnar head. The presence of this band increases the probability that the real ulnar head is suppressed, not fused, in the Virginian Opossum, and therefore the muscle shown in fig. 3 is the result of an artificial division of the adductor. Professor Cunningham,¹ in his description of the hand of the Vulpine Phalanger, expresses the opinion which I have given above, viz., that the real ulnar belly of flexor brevis pollicis is suppressed;—he regards, however, the muscle corresponding to *a^{ba}* and *a^{ba}* (fig. 2) as the ulnar head of flexor brevis minimi digiti.

In *Macacus nemestrinus* there are four adductors, those to the index and ring digits being small. There is a broad triangular adductor pollicis inserted directly into the radial side of base of the first and second² phalanges of the thumb. From the part

¹ *Op. cit.*, p. 25.

² If this condition is constant in *Macacus* it shows a curious reappearance of a reptilian character in a high form of mammal. A similar condition (insertion into second phalanx) of the adductor minimi digiti pedis is described by both Ruge and Cunningham in the *Ornithorhynchus*. The latter also describes the

arising from the carpus a fasciculus diverges to be inserted into the *radial* sesamoid (compare *a^{1a}* in *Cynocephalus*). These two parts are intimately connected for at least the proximal half of their length. On separating these two the deeper fibres of the large triangular portion are seen to be inserted into the ulnar sesamoid; as the origin of these latter fibres is from the ligaments at the base of the second and third metacarpal bone they evidently form a part of the real adductor, and cannot be regarded as a flexor brevis. Flexor brevis radial head and opponens pollicis are similar to the same in Man, but there appears to be no trace of an ulnar head of flexor brevis. The muscles of the little finger differ in only one point from those of the Marmoset; the radial head has become rather the larger, and more distinctly resembles the homologous muscle in Man (third palmar interosseous). The condition of paired flexores breves for the three middle digits, however, has vanished, and in its place we have an arrangement of "interossei" similar to that in Man.

In *Colobus* the thumb is rudimentary, appearing only as a minute projection before the skin is reflected; it possesses, however, a metacarpal bone and phalanges, the distal phalanx being the size of a pin's head. There is no long flexor tendon, but the short muscles are remarkably distinct and well-defined. Abductor pollicis is rather weak, but otherwise typical. The flexor brevis pollicis arises by a pointed tendinous process from the annular ligament near the os trapezium, and divides into two bellies, of which the radial is rather the larger; these are inserted with the abductor and adductor respectively. The sesamoid bones appear to be absent. A very few fibres of the radial head are inserted into the metacarpal bone, but there is a slip from the *ulnar* head which forms an opponens; it is inserted on the ulnar side of the middle line of the shaft. The broad, flat triangular adductor arises from the fascial structures over the middle metacarpal bone, and is separated by a comparatively wide interval from the flexor brevis.

There is a "flexor brevis" minimi digiti (*a^{5a}*), from the deeper part of the origin of which an opponens is formed. The

insertion of the adductores into the ungual phalanges in the pes of *Echidna* also a slip to the ungual phalanx of the hallux in *Cuscus* (*op. cit.*, p. 57).

latter is inserted into the whole length of the metacarpal bone of the little finger. There is a true flexor brevis separated from the two preceding muscles by the deep branch of the ulnar nerve; its radial belly forms the "third palmar interosseous;" its ulnar belly is very small and forms an opponens, a few fibres reaching as far as the head of the metacarpal bone; it is overlaid and dwarfed by the greatly developed opponens derived from the palmar layer of adductores.

In *Cynocephalus anubis* (fig. 5) there is a large adductor pollicis arising from a strong fibrous band over the middle metacarpal, and from the ligaments over the bases of index and middle metacarpals, a slip (a^1a) passes from it to be strongly inserted into the radial sesamoid. There is a powerful radial head of flexor brevis (f^1r) arising from the anterior annular ligament and os trapezium; from the deeper part of its origin the ulnar head springs. It is about one-fifth the size of the radial head, and is inserted along the middle line of shaft of metacarpal, its most distal fibres inclining to the ulnar side, to be inserted close to the ulnar sesamoid but not reaching it. It will be remembered that a similar muscle forms part of the ulnar head in *Colobus*; this muscle is concealed by a^1a in the figure; it is separated from the latter by a strong fibrous sheath. Turning to the little finger, we find a "flexor brevis" (a^2a) arising from the annular ligament close to the tip of the very short unciform hook; intimately blended with its deeper fibres of origin we find an opponens (a^2op) inserted into the distal two-fifths of ulnar border of shaft of fifth metacarpal. The deep branch of ulnar nerve separates the foregoing from the true flexor brevis, which arises chiefly from unciform and diverges to form "third palmar interosseous" (f^3r), and an opponens inserted into the whole length of the shaft of the metacarpal (f^3op). The adductor (a^3) is in this form rather widely separated from (a^2a).

In the Chimpanzee the "flexor brevis" minimi digiti (fig. 7. a^5a) has the same origin and insertion as in Man; from its deeper fibres of origin an opponens (a^5op) is developed, which is inserted into the distal four-fifths of the fifth metacarpal on its ulnar border. The deepest part of the origin of this opponens, from the base of the unciform hook, is united with the pointed proximal extremity of the origin of the adductor minimi

digiti; the latter has also a thin scattered extensive origin from the fascia over the ring metacarpal. The radial head of flexor brevis minimi digiti (f^{5r}) resembles the "third palmar interosseous" in Man; a few fibres spring from the unciform. Closely associated with this origin, the ulnar head (f^{5u}) arises from base of unciform hook, and is inserted into the proximal fifth of the ulnar border of shaft of fifth metacarpal; it is slightly blended at its insertion with the other opponens (a^{5op}), but quite separable at origin; the deep branch of the ulnar nerve passes between them. The adductor pollicis arises from a fibrous band, which passes from the head of the ring metacarpal to the base of the middle metacarpal, and from the ligaments over the bases of the middle and index metacarpals; it shows a slight division into adductor obliquus and a. transversus. There is no trace of any slip like a^{1a} in *Cynocephalus*. There is a well-developed radial head of flexor brevis pollicis arising from the annular ligament close to the os trapezium, and inserted with the abductor. The inner head is represented by a sharply-defined glistening fibrous band, which arises from the extreme base of the thumb metacarpal, and is inserted with the adductor in ulnar side of base of proximal phalanx of thumb. In the specimen dissected (a young female) there were no sesamoid bones.

In the Orang there is a condition of the muscles of the little finger more resembling Man than any other animal I have examined. The "flexor brevis" minimi digiti (a^{5a}) is relatively larger than in Man, and the opponens which arises in connection with it is inserted into the entire length of the shaft of the fifth metacarpal bone. The adductor of the thumb is the only adductor present, unless the others are represented by a very tough fibrous tissue which covers the interossei and the deep branch of ulnar nerve. Flexor brevis minimi digiti radial head is as in Chimpanzee, but the ulnar head appears to be entirely wanting. The adductor pollicis has the same connections as in man, but the slip which passes to the radial sesamoid (a^{1a}) is wanting. The flexor brevis pollicis arises from the os trapezium and annular ligament, and divides into two fleshy bellies, a small ulnar, and a much larger radial, which are inserted into corresponding sides of the proximal phalanx, and separated by the slender long-flexor tendon (t , fig. 6).

In Man the "flexor brevis" minimi digiti (*a⁵a*) is relatively smaller than in any of the other animals, and is frequently wanting; intimately connected with its deeper fibres of origin from the unciform hook we find an opponens, which is usually inserted into the distal four-fifths of the shaft of the metacarpal (as in the Chimpanzee), but may be limited to the lower half or even less (fig. 8, *a⁵op*). Arising from the shaft of the fifth metacarpal, and in most cases from the unciform¹ is the radial head of the true flexor brevis ("third palmar interosseous," *f⁵r*) and closely associated with the unciform origin and inserted into the proximal fifth of the metacarpal bone there is a small muscle (*f⁵op*) separated by the deep branch of the ulnar nerve from the first mentioned opponens, and quite distinct from the latter at its origin. In the specimen from which fig. 8 was drawn this muscle was unusually large, and at its origin *formed one muscle with the third palmar interosseous*. In the thumb we find a very powerful adductor, whose origin is pierced by the deep palmar arch, the division into adductor transversus and a. obliquus being thus indicated;² the a. obliquus is described in English text-books as the deep or inner head of flexor brevis. From the adductor obliquus a strong bundle of fibres³ passes to the radial sesamoid of the thumb; this is identical with *a¹a* in Cynocephalus. The radial head of flexor brevis is strong, and arises from the lower border of the annular ligament close to its attachment to the os trapezium. The true ulnar head (interosseus primus volaris) arises from the extreme base of the metacarpal bone of the thumb, and is inserted with the adductor, some fibres being often prolonged on to the dorsum of the phalanx to join the long extensor tendon.

It is evident from the above descriptions that the so-called "flexor brevis" minimi digiti of the human hand is not homologous to the muscle of the same name in the foot; the flexor brevis minimi digiti of the foot lies close to the metatarsal bone and beneath the deep division of the external plantar nerve, while in the hand "flexor brevis" is superficial to the deep branch of ulnar nerve. Professor Cunningham⁴ has shown that

¹ Henle, *Muskellehre*, p. 246.

² Bischoff, *op. cit.*, p. 20.

³ See Quain's *Anatomy*, 9th edition, vol. i. p. 226.

⁴ *Op. cit.*, p. 116.

the flexor brevis minimi digiti of the foot and the "third plantar interosseous muscle" are the fibular and tibial bellies of the same muscle. In the Opossum (fig. 4 f⁵), and in many of the mammalian feet figured by Professor Cunningham;¹ this condition is very evident, the two bellies being symmetrical and the insertion on each side phalangeal. In the Chimpanzee I found in both feet the flexor brevis minimi digiti and "third plantar interosseous" arising together by a pointed tendinous origin from the sheath of the peroneus longus tendon, as far back as the ridge on the cuboid bone; the "interosseous" had an additional origin from the shaft of the fifth metatarsal. The fibular belly was inserted into the shaft of the metatarsal, its only connection with the phalanx being through the abductor tendon, into which a few fibres were inserted. A very similar condition to this is described in Professor Cunningham's notes on the dissection of a negro foot from Sierra Leone;² the insertion into the phalanx of the flexor brevis, however, was present. In European feet the following is a frequent condition of the flexor brevis minimi digiti:—The greater part of the muscle arises (more or less associated with the third plantar interosseous) from the sheath of peroneus longus, the remainder arising from the base of fifth metatarsal; the insertion is partly into the metatarsal, partly into abductor tendon, and the remainder directly into the phalanx.

While in the foot the fibular belly of flexor brevis minimi shows a tendency to become reduced to an opponens, this tendency is more pronounced in the hand. In the following animals we find the insertion becoming more and more proximal, and the size of the muscle diminishing *pari passu*:—Cat, Marmoset, *Macacus*, *Cynocephalus*, *Colobus*, Man, Chimpanzee, Orang. In the latter it appears to be absent altogether. In the first three we find the opponens (*a⁵op*) (which lies superficial to the deep ulnar nerve) absent. In the others it shows a gradual increase in size, functionally replacing the deeper muscle. Again in the Cat the "flexor brevis" (of human anatomy) is absent but present in all the rest, and in the Cat alone (in this series) we find the true flexor brevis (ulnar head) with a phalangeal insertion.

¹ *Op. cit.*, plate viii. fig. 1, f⁵; plate xi, figs. 1, 6, and 10.

² Unpublished as yet.

Having now demonstrated the true flexor brevis, let us examine the so-called "flexor brevis" of man. It corresponds in every way with (a^5a) in *Cynocephalus*, *Opossum*, and *Chimpanzee* (figs. 5, 2, and 7). In the *Opossum* its origin is continuous with the adductor minimi digiti, the gap usually found between their origins being occupied by a muscle (a^5a'), which is evidently only a deeper fasciculus of a^5a . This deeper fasciculus, which is phalangeal in insertion, shifts its insertion to the metacarpal bone in higher forms, and appears as a^5op in *Cynocephalus*, *Chimpanzee*, and *Man*. We have thus in the *Opossum* what is practically one sheet of muscle a^5 , a^5a' , and a^5a separated by the deep branch of ulnar nerve from the layer of flexores breves. It appears probable that the adductor minimi digiti extends both its origin and insertion towards the ulnar side of the hand, and that the pressure of the long flexor tendon (or tendons) afterwards divides the insertion into two slips,² the deeper fibres of the ulnar part afterwards contracting an insertion into the metacarpal bone. The pressure of the tendon and the greater development of the unciform process then separates the origin³ also, so that the ulnar border of the adductor minimi digiti becomes divorced from the rest, and we call it "flexor brevis" and *opponens minimi digiti* in Human Anatomy. In *Man* and in *Orang* the typical adductor minimi vanishes, and the aberrant part remains as its only representative.

In *Man*, *Macacus*, and *Cynocephalus*, we find an indubitable part of the adductor pollicis (a^1a) passing to be inserted into the radial sesamoid; in some human hands, on raising the long flexor tendon, the adductor fibres are seen to pass in an almost continuous sheet across the base of the phalanx from the ulnar to the radial sesamoid, some small twigs from the arteria princeps pollicis being the only separation. The pressure of the single flexor tendon of the thumb has been insufficient to separate the insertions in some cases, or in any case to separate the origins.

The travelling in a radial direction of the adductor pollicis causes it to overlies, to functionally replace, and therefore to

¹ In the more primitive types the muscles in the hand are powerful, while in higher forms there is a tendency for the muscular structures to retreat to the fore-arm, the hand being occupied by tendons.

² In *Cynocephalus*, in which the flexor tendons are enormously strong, we find a wide separation between a^5 and a^5op (fig 5)

dwarf, the true ulnar head of flexor brevis. As the valuable guide of nerve relation is absent on the radial side of the hand, it is difficult to say in most cases whether the ulnar head becomes fused with adductor pollicis or aborts entirely. I believe that fusion rarely if ever occurs, as we find either a ligamentous rudiment of the true ulnar head of flexor brevis (as in Chimpanzee and Vulpine Phalanger), or a complete absence of any fibres arising in common with the radial head or from the base of the metacarpal bone of thumb (as in *Macacus*). It is curious that the true inner head should be better represented in some of the higher primates (Man, Orang) than in many of the lower monkeys.

Bischoff¹ describes "two heads of the flexor brevis pollicis, the inner somewhat weaker and deeper than the outer," in *Cynocephalus maimon*, *Cercopithecus sabäus*, *Macacus cynomolgus*, *Pithecia hirsuta*, and *Hapale penicillata*. I could not find any true inner head in *Macacus nemestrinus* or in *Hapale*, and from a careful inspection of his figures of *Cynocephalus maimon* and comparison with *Cynocephalus anubis*, I believe that what he calls the inner head of flexor brevis is identical with (*a*^{1a} fig. 5), being a part of the adductor inserted into the radial sesamoid.

While the dissections described above have shown that the so-called "flexor brevis" minimi digiti of the hand of Man is a different muscle to the true flexor brevis, there are two possible views of its morphology besides the one advocated above:—

- (a) That it is a part of the abductor.
- (b) That it is the division of the flexor brevis digitorum manus to the little finger.

(a) In favour of the first view, it may be urged that the origin of the corresponding muscle on the radial side (abductor pollicis) has a great tendency to travel ulnarwards along the annular ligament, even passing the middle line in some cases. On the other hand, the nerve relation is a strong argument against this view. In *Cynocephalus*, where a second slip of the abductor takes origin from the annular ligament (fig. 5), the normal nerve relation is still preserved. The absolute continuity of origin of the "flexor brevis" (*a*^{5a}) with the normal adductor, which has

¹ *Op. cit.*, pp. 90, 91.

been shown in Virginian Opossum, Vulpine Phalanger, and even in so high a form as the Chimpanzee, is another reason against regarding "flexor brevis" as part of the abductor.

(b) In favour of the second view, the fact may be noticed that in the foot the tendons of the short flexor are not always perforated. In the Chimpanzee I found the tendon to the little finger inserted into the floor of the flexor sheath, on the fibular side of the base of the *proximal* phalanx of the little toe, and I have seen the same condition in Man. In the toes of Ornithorhynchus, Cunningham has shown that none of the tendons of the short flexor are perforated. A strong argument against this view, however, is the presence of a flexor brevis digitorum manus to the little finger in the Opossum (*fbdm*, fig 2), coexisting with *a^{5a}*. In the foot of the Opossum there is a perforated tendon for the fifth toe coexisting with the muscle (*a^{5a}*, fig. 4), and it appears probable that the latter is the homologue of the "flexor brevis" minimi digiti of the hand.

EXPLANATION OF PLATE XXI.

Fig. 1. Manus of Cat. *f¹* to *f⁵*, flexores breves,—*f¹* has only the radial head; *u*, deep branch of ulnar nerve passing under pisi-uncinate ligament, and then under two of the adductores, *a⁵* and *a²*; *a¹*, adductor pollicis; *abd⁵*, abductor minimi digiti.

Fig. 2. Manus of Virginian Opossum. *a¹*, *a²*, *a⁴*, *a⁵*, adductores; *a^{5a}* and *a^{5a'}*, parts of adductor minimi digiti whose insertion has wandered to ulnar side of fifth digit; *u*, ulnar nerve, its deep branch passing under the adductores; *fbdm*, flexor brevis digitorum manus reflected; *f^{1r}*, radial head of flexor brevis pollicis; *abd¹*, abductor pollicis.

Fig. 3. Deeper dissection of manus of Opossum. *f¹* to *f⁵*, flexores breves. The deep branch of ulnar nerve is shown passing superficial to all of these.

Fig. 4. Pes of Virginian Opossum. *epn*, deep branch of external plantar nerve; *f^{1t}* and *f^{1f}*, tibial and fibular heads of flexor brevis pollicis.

Fig. 5. Manus of *Cynocephalus anubis*. *f^{5r}*, radial head of flexor brevis minimi ("third palmar interosseous"); *f^{5op}*, opponens minimi derived from true flexor brevis; *a^{5op}* opponens from layer of adductores; *a^{5a}*, "flexor brevis" minimi digiti; *op¹*, opponens pollicis; *a^{1a}*, part of adductor pollicis inserted into radial sesamoid; *t*, tendon of flexor longus pollicis.

Fig. 6. Thumb of Orang. *f^{1r}* and *f^{1u}*, radial and ulnar heads of

flexor brevis pollicis, having a common origin, but separated at their insertion by *t*, the slender tendon of flexor longus pollicis.

Fig. 7. Diagram of the adductores of the manus of a Chimpanzee. *d*⁴, fourth dorsal interosseous; *a*¹*ob*, adductor obliquus; *a*¹*tr*, adductor transversus; other letters as before. Observe that the origins of *a*⁵ and *a*⁵*op* are absolutely continuous for a short distance, and that *a*⁵*op* and *a*⁵*a* are united by half their length.

Fig. 8. Short muscles of the little finger in Man, showing an unusually large part of the opponens minimi digiti derived from the true flexor brevis; *f*⁵*r*, "third palmar interosseous." The "flexor brevis" minimi digiti (of human anatomy) was absent in this case.

ON THE NATURE OF THE RELATIONSHIP OF UREA FORMATION TO BILE SECRETION. By D. NOËL-PATON, M.D., B.Sc., F.R.S.E., *Biological Fellow of the University of Edinburgh.*

(From the Physiological Laboratory of the University of Edinburgh.)

(Continued from p. 531.)

IN confirmation of the conclusion that urea formation and bile secretion are related to one another through their inter-dependence upon destruction of blood-corpuscles, I here give a further experiment, in which toluylendiamin was used as the hæmolytic agent. This experiment is especially valuable, because the disturbing influence of increased production of hæmocytes does not appear to have obscured the extent of destruction. It was only some days after the destruction of corpuscles had reached its greatest extent that increased production fairly established itself. This is probably to be accounted for by the fact that a dog considerably older than those used in my previous experiments was employed.

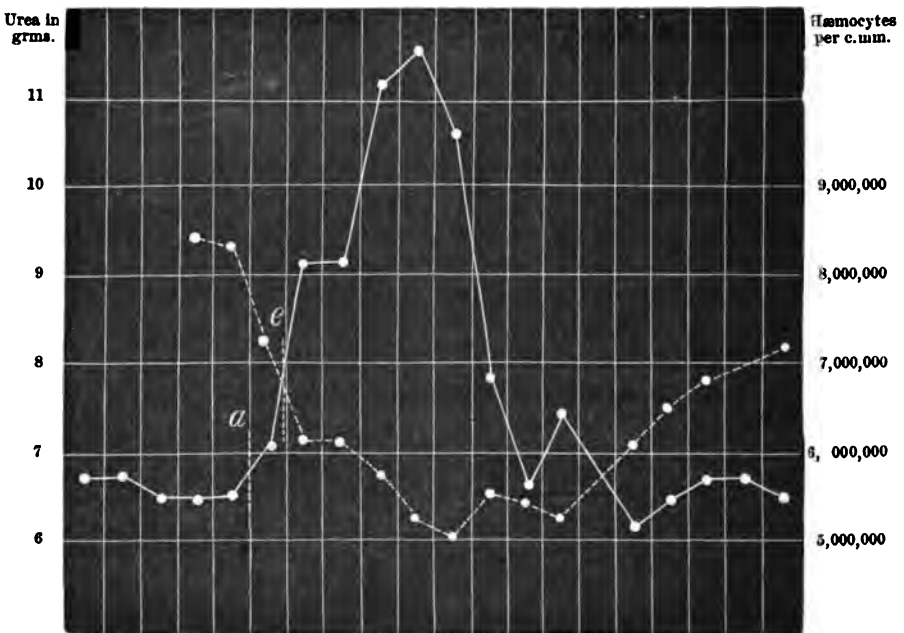
Exp. VI.

For this experiment an old black retriever bitch, weighing 15·876 kilos., was used. The subjoined table and fig. 5 show the influence of toluylendiamin on the urea production and on the number of blood-corpuscles. On the sixth day of the experiment 0·4 grm. of the drug was administered, while 0·3 grm. was given on the following day. On the seventh day the dog was distinctly jaundiced, and the urine was of a dark port wine colour and contained bile acids and pigments. On the eighth day the jaundice was more marked and general, but by the ninth day it had somewhat diminished. Throughout the experiment the dog seemed perfectly well and took its food greedily. Calculating as in the former experiments we find that a dog of this weight has 1221 grms. of blood and 168 grms. of hæmoglobin. Between the fifth and the eleventh day the corpuscles fell from 8,390,000 to 5,060,000—a fall of 39·69 per cent. Thus throughout the body 66·7 grms. of hæmoglobin must have been set free, and, supposing this to be entirely broken up into urea, bilirubin, &c., we should expect to find a formation of 20·2 grms. of urea above the normal.

Before the administration of the drug 6·645 grms. of urea were daily excreted, and during the six days following its administration the production of urea in excess of the normal was 18·588. On the seventh day 1·251 grm. of urea in excess of the normal were excreted, making in all 19·839—only 0·361 grm. less than the amount calculated from the disintegration of hæmocytes.

Day of Exp.	Urine in c.cs.	Sp. G.	Urea in Grms.	Hæmocytcs per c.mm.	Remarks.
1	{ 525	1013	6·741	...	Weight on 5th = 15·87 kilos.
2	{ 525	1013	6·741	...	
3	{ 520	1013	6·554	...	
4	{ 460	1014	6·596	8,500,000	Diet—Oatmeal = 170 grms. Milk, . 320 c.c.
5	{ 460	1014	6·596	8,390,000	
6	{ 500	1015	7·070	7,320,000	0·4 gm. Toluylendiamin. 0·3 gm. Toluylendiamin.
7	{ 490	1018	9·156	6,185,000	
8	{ 490	1018	9·156	6,165,000	
9	{ 400	1018	11·280	5,870,000	
10	580	1015	11·600	5,250,000	
11	620	1014	10·626	5,060,000	
12	470	1016	7·896	5,510,000	
13	520	1013	6·635	5,410,000	
14	480	1015	7·566	5,280,000	
15	
16	580	1013	6·158	6,030,000	
17	400	1015	6·560	6,525,000	
18	{ 500	1014	6·726	6,690,000	
19	{ 500	1014	6·726	...	
20	600	1012	6·500	7,170,000	

FIG. 5.



Exp. VI. — Influence of tolmyglendiamin on urea production and on number of hæmocytcs per c.mm. 0·4 grms. given at *a*, and 0·3 grms. at *e*.

Even if we refuse to accept the hypothetical decomposition of the hæmoglobin molecule given above, the very close relation ship between the extent of the destruction of blood-corpuscles and the increase in the urea excretion shown by these experiments clearly indicates the existence of a definite connection between these two processes.

DIRECT ACTION ON THE HÆMOCYTES OF DRUGS INCREASING UREA PRODUCTION AND BILE SECRETION.

As before stated, Afanassiew has connected the cholagogue action of toluylendiamin with its direct destructive influence upon the blood-corpuscles, while Paschkis has demonstrated that these most powerful hæmolytic agents—the salts of the bile acids—stimulate bile secretion in a very marked degree.

By observing the action of salicylate of soda, of benzoate of soda, of colchicine, and of mercury on the hæmocytes, I have endeavoured to ascertain whether or not their double action on bile secretion and urea production can to any extent be explained by their primary direct influence on the blood-corpuscles.

For this purpose the action of these substances outside the body, and in some cases in the living animal, has been studied.

Observations outside the body of the action of these drugs are absolutely essential, since changes produced in the corpuscles after their introduction into the living body are not necessarily due to the direct action of the agents. Specially important is the demonstration of these changes in such a research as the present, when from the increased secretion of bile induced the possible action of bile acids and their salts must be carefully excluded. My object has been merely to ascertain if the drugs above mentioned have any hæmolytic action, and I have not considered it expedient to describe at length the various changes which occur in the course of the disintegration of hæmocytes—a line of histological research which would, I believe, throw some important light on the minute structure of the red blood-corpuscle.

In such a research various precautions are necessary. In the first place, the solution employed must have a neutral reaction,

since any degree of acidity or alkalinity tends to destroy the corpuscles. Secondly, it is necessary to employ solution of the same specific gravity as the blood-serum—1025—or to use such a solvent as a 0·75 per cent. salt solution in which corpuscles remain unchanged. This salt solution is especially useful where dilute solutions of the reagent have to be employed.

The action of these substances has been studied not only on the mammalian, but also on the amphibian blood; but since their action on the latter is precisely similar to their influence on the former, I have not deemed it necessary here to describe it in detail, and have confined myself entirely to the changes observed in the human blood.

The mode of experiment was as follows:—A drop of the solution was placed on the finger, which was pricked through this. The blood was mixed with the solution, and the mixture was transferred to a shallow cell, covered and at once examined, usually under a Zeiss F lens.

SALICYLATE OF SODA.

On the action of salicylic acid and salicylate of soda on the red blood-corpuscles outside the body several observations are already recorded.

Chirone, in a paper entitled "*Acido Salicilico e. Salicilate*" (*Il Movimento med. e. chir.*, 11-12 maggio, quoted in *Jahresb.* for 1878, p. 408,) states that the toxic action of this drug depends upon its destructive action upon the hæmocytes.

Cotton, "*Act. de l'acide salicylique sur le Sang et en particulier sur les globules rouges*" (*Lyon Méd.*, t. 1. p. 557, quoted by Prudden) shows that with a 3 per cent. solution the red corpuscles become globular and that the hæmoglobin is decomposed.

Prideaux (*Practitioner*, Sept. 1878, p. 171) states that it has no influence upon the hæmocytes, but that the movements of the leucocytes are diminished.

Thiersch (*Volkmann's Klin. Vorträge*, Nos. 84 and 85, p. 657) finds that salicylic acid destroys the red blood-corpuscles.

Prudden (*American Medical Journal* for 1882, p. 64) describes very carefully the influence of salicylic acid dissolved in a 0·5 per cent. salt solution upon the hæmocytes. He finds that a solution containing 1 part in 500 causes a rapid disintegration of the corpuscles, but that in more dilute solutions it acts merely like other dilute acids. He also notices that it acts more rapidly upon the corpuscles of the frog than upon the mammalian corpuscle.

A. Outside the body.

Solutions of different strengths were employed, but with the stronger solutions disintegration of the corpuscles occurred so rapidly that it was impossible to study the various changes. A 1 per cent. solution in 0.75 per cent. salt solution may be employed with advantage.

On allowing a drop of this solution to mix with a drop of blood the following changes occur:—

1. Large blunt crenations appear round the periphery of the disc.
2. These crenations become sharper and longer, and the corpuscles shrink in size and assume a spherical form.
3. The spines next become more numerous, entirely covering the surface of the corpuscle, at the same time they become shorter.
4. The spines finally disappear, leaving a small highly refracting deeply pigmented sphere.
5. The hæmocyte now slowly increases in size, becomes paler, and on close examination it is seen to be granular—the granules appearing to be in an active state of motion within the hæmocyte.
6. The granules become more and more apparent, and grow larger and larger and seem to collect the pigment around them, so that we have a colourless cell with a thin layer of pigment under the membrane and masses of pigment throughout the cell.
7. The pigment is gradually dissolved out—colouring the blood-serum, and leaves within the cell colourless masses of the intracellular stroma.
8. These masses become less and less distinct, and finally an almost homogeneous, colourless, transparent, spherical shadow is left, which requires for its detection very careful focusing.

Different corpuscles are seen to have a very different resisting power in regard to the action of salicylate of soda. Some corpuscles break down at once, while others hold out for long after the majority have been reduced to shadows.

B. In the living body.

Exp. I.

A female, aged 15 years, and weighing 40·8 kilos., who was suffering from favus but who was otherwise healthy, was employed in this and in the next experiment. The diet was as nearly as possible uniform, and at 12.30 each day the number of hæmocytes per c.mm. were estimated with Gower's hæmocytometer.

Between 2 P.M. on April 7th and 10 P.M. on April 8th, 13 grms. of salicylate of soda were administered in 20-grain doses. On the morning of the 8th well-marked symptoms were induced. The accompanying table shows, that under the influence of salicylate of soda a fall of 300,000 per c.mm. occurred in the number of corpuscles:—

Date.	No. of Hæmocytes per c.mm.	Remarks.
1885.		
April 5th	4,825,000	{ 13 grms. salicylate of soda.
" 6th	4,900,000	
" 7th	4,870,000	
" 8th	4,870,000	
" 9th	4,570,000	
" 10th	4,650,000	
" 11th	4,720,000	
" 12th	...	
" 13th	4,740,000	

Exp. II.

The same individual was used as in Exp. I. and the experiment was in every way, with the exception of the doses given, exactly the same as the last. The administration of the drug was commenced at 12 noon on the 28th. On the evening of the 29th well-marked symptoms were induced.

The following results were obtained:—

Date.	No. of Hæmocytes per c.mm.	Remarks.
April 27th	4,850,000	7·2 grms. of sod. sal. in 24 hrs. 7·2 grms. of sod. sal. in 24 hrs.
" 28th	4,850,000	
" 29th	4,695,000	
" 30th	...	
May 1st	4,625,000	
" 2nd	4,060,000	Faint traces of salic. in urinc.
" 3rd	4,720,000	
" 5th	4,750,000	

Exp. III.

A setter bitch, weighing 11·80 kilos. and recovering from the anæmia induced by the administration of pyrogallie acid, was used. The diet was fixed.

Date.	No. of Hæmocytes per c.mm.	Remarks.
May 14th	5,400,000	
„ 15th	5,320,000	6 grms. salicylate of soda.
„ 16th	5,000,000	6 grms. salicylate of soda.
„ 17th	4,555,000	
„ 18th	5,105,000	

These three experiments, yielding results so entirely uniform, clearly show that in the mammalian body the administration of even comparatively moderate doses of salicylate of soda is followed by a considerable destruction of blood-corpuscles.

BENZOATE OF SODA.

The benzoates like the salicylates belong to the carbolic acid group of pharmacological substances, most of which, as indicated by Harnack (*Arzneimittellehre*, s. 288), exert a destructive influence on the blood-corpuscles. I have been unable, however, to find any experiments on the direct action of the benzoates in the blood.

When a 5.5 per cent. solution of benzoate of soda (sp gr. 1025) is mixed with a drop of human blood, the following changes occur in the corpuscles:—

1. Some assume a globular form, and become larger and paler.
2. A great number are enlarged and paler with a faintish more or less crenated outline. Their form becomes irregular, varying from almost spherical to fusiform.
3. The largest number become somewhat reduced in size, lose their biconcave form, appear bounded by a strong dark border, and are markedly crenated. When a number of these are together a curious oscillatory movement may be seen, closely resembling Brownian movement.

If such a preparation be placed for some time in a warm moist chamber a large number of the corpuscles are converted into shadows, while all stages between such shadows and the small crenated corpuscles may be studied. Under the cover-glass these changes go on much more slowly than without it. In this respect

benzoate of soda appears to resemble toluylendiamin, which according to Afanassiew (*loc. cit.*) requires the free ingress of air to the preparation to enable it to exert its destructive influence upon the hæmocytes.

In all these observations check experiments, with blood mixed with 0.75 per cent. salt solution, showed no destruction of corpuscles.

Benzoate of soda is therefore undoubtedly a hæmolytic agent, but not of such power as the salicylate.

COLCHICINE.

I can find no observations on the direct action of colchicine on the blood-corpuscles. Schroff (*Lehrbuch der Pharmacologie*, p. 615) describes the condition of animals poisoned with colchicine as follows:—

“Am constanten fand sich Enteritis bisweilen Gastritis und immer ein dickes, peschwarzes, theerartiges, schmieriges Blut, das die Höhlen des linken Herzens und die obere und untere Hohlader bis in ihre Verzweigungen, die dem Hirn, der Leber und der Niere angehören erfüllte.”

All subsequent writers have merely quoted this observation of Schroff.

A. Outside the body.

A 5 per cent. solution of perfectly neutral colchicine dissolved in 0.75 per cent. salt solution was used.

The following changes were observed:—

1. The corpuscles become cupped, a convexity taking the place of the concavity on one side.
2. The lips of the cup approach one another and become irregular.
3. The corpuscles become spherical, some small and dark, others larger and paler.
4. The large pale hæmocytes become shadows simply by losing their colouring matter.

Some of the smaller ones enlarge and throw out processes: these processes are either (1) long transparent filiform vibrating tails, sometimes markedly articulated, almost moniliform at other times with no apparent joints, but always with a somewhat club-shaped head; or (2) round,

clear, and spherical. Both forms are to be seen in the one corpuscle. These processes often break off and cause a granular appearance of the serum in which the corpuscles float, at other times they remain attached.

5. The pigment slowly dissolves out till only a layer inside the cell membrane is left.
6. This in turn, too, disappears, and nothing is left but a shadow, often with processes attached.

B. Within the body.

The method of enumerating the corpuscles per c.mm., employed in my experiments on the action of salicylate of soda upon the blood in the living mammal, was unsuited for the investigation of the blood-changes induced by such a drug as colchicine, which by its well-known cathartic action causes a concentration of the blood as shown by Malassez.

Another method of experiment had to be adopted:—

Exp. I.

A large male cat received no food for twenty-four hours. At 11 o'clock on May 5th 0·1 grm. of colchicine, procured from Messrs Hopkin & Williams, London, dissolved in about 20 c.cs. of water was administered.

During the afternoon the cat had several mucous evacuations of the bowels, and vomitted some glairy matter. In the evening it was dull; it died on the morning of the 6th.

The thorax was opened, and some blood taken from the right auricle was at once examined; this contained a very large number of shadow corpuscles arranged in groups. Blood taken from the femoral vein, and from the lower part of the vena cava, also showed the presence of these shadows, but not in such large numbers as in the heart.

The right side of the heart was full of fluid blood of a very dark colour, which coagulated on being placed in a glass vessel.

This experiment clearly shows that colchicine within the animal body destroys the red blood-corpuscles.

PERCHLORIDE OF MERCURY.

On the action of the salts of mercury on the hæmocytes outside the body, I can find only one investigation. This is by Polotebnow (*Virchow's Arch.*, Bd. xxxi. s. 35), who employed a solution of albuminate of mercury, 1 c.mm. of which contained from 0·014 to 0·015 grm. of perchloride of mercury. As a result of his investigations he concludes that:—

1. Under the influence of concentrated solution of albuminate of mercury, the blood-corpuscles after their round form is once altered have lost the capacity to resume their original shape, either through a loss of the elasticity of their membrane or in consequence of some other cause.
2. In a solution of albuminate of mercury the corpuscles are very quickly destroyed, the rapidity being in proportion to the amount of mercury present, and being also more rapid when the blood is shaken up with air, or when the temperature is raised for thirty or forty minutes to 37° or 38° C.
3. Under the influence of mercury the corpuscles quickly lose their pigment, and the more concentrated the solution the more rapidly does this take place.
4. The absorbent power of the blood for oxygen is also diminished.

Of the many investigations on the action of mercury on the blood-corpuscles in the living body, I can find only one of any scientific value. The majority have been made on syphilitic

Exp. IV.

Date.	Hæmocytes per c.mm.	Weight of Rabbit.
May 5th	4,480,000	2·120 kilos.
0·001 grm. of perchloride of mercury given daily hypodermically from 5th onwards.		
May 8th	4,200,000	2·010 kilos.
„ 9th	4,000,000	1·900 „
„ 11th	4,000,000	1·800 „
Diarrhœa occurred on the 12th, and the corpuscles rose to—		
May 12th	5,202,400	1·870 kilo.
The treatment was stopped till the diarrhœa ceased, and was then continued.		
May 15th	3,363,800	1·736 kilo.
„ 16th	3,200,000	1·676 „
The dose was progressively increased.		
„ 17th	3,140,000	1·660 „
„ 18th	3,000,000	1·650 „
„ 19th	2,900,000	1·500 „
„ 20th	2,800,000	1·460 „
„ 21st	2,700,000	1·444 „
„ 22nd	Animal died.	

patients, with small doses of the drug extending over a lengthened period, so that as direct evidence of the action of the drug on the corpuscles they are of no value.

Wilbowchewitch (*Arch. de Physiologie*, t. i. p. 530) records four experiments made upon rabbits, which clearly show that under large doses of perchloride of mercury a very marked diminution in the number of blood-corpuscles per c.mm., occurs. The preceding table gives the results of his fourth experiment.

Such experiments are only of value when taken along with observations in the hæmolytic action of mercury outside the body, since without such observations it would not be fair to conclude that any increased destruction, and not merely a diminished production, had occurred.

The chief difficulty in the way of studying the action of mercury upon the blood-corpuscles outside the body, is that nearly all the salts of this metal cause coagulation of albumin. The mercuric potassic iodide in dilute solution has not this action, and I have therefore employed it in the following observations.

I had previously ascertained from a number of experiments that the iodide of potassium has absolutely no action on the red corpuscles, and that the chloride of potassium is also inert.

I therefore consider it a fair deduction, that any action which the mercuric potassic iodide may exert is due to the mercury it contains.

A solution composed of—

1 grm. of mercuric chloride,
3 grms. of potassic iodide, and
60 c.c. of water,

was prepared, and was diluted with 60 c.c. of a 0.75 per cent. salt solution, as its action without this dilution was so rapid as to prevent any observations on the nature of the changes induced.

When this solution is added to a drop of blood, the hæmocytes are seen to swell up and to lose their biconcave form, while the pigment disappears leaving the cell membrane enclosing the intranuclear network. Very frequently the membrane collapses and the corpuscle is represented by a shrivelled shadow.

I have not thought it necessary to repeat Wilbowchewitch's observations. In fact, the extremely poisonous nature of the salts of mercury render such observations difficult.

It would thus seem that the influence of these drugs on bile secretion and urea formation may be explained by their destructive influence on red blood-corpuscles, hæmoglobin being set free and excreted by the liver as already described. Such a direct influence on the blood-corpuscles is rendered all the more probable by their absorption into the very slow hepatic blood-stream, and also through their probable re-entrance into the liver, after excretion in the bile, through the entero-hepatic circulation.

From these observations I would conclude :—

1. That the destruction of blood-corpuscles must be considered as a powerful stimulant to the secretion of bile, the liver having as one of its functions the elimination from the system of effete hæmoglobin.
2. That urea production also is increased by the destruction of blood-corpuscles.
3. That bile secretion and urea formation bear a direct relationship to one another, and that this relationship is due to the dependence of both upon destruction of hæmocytes.
4. That the hæmolytic action of salicylate of soda, of benzoate of soda, of colchicine, and of perchloride of mercury, as well as their influence in increasing the production of urea, is due in great measure at least to their direct hæmolytic action.

The connection of urea production with the destruction of hæmocytes naturally suggests the question—How much of the total urea produced in the animal body in its normal condition is derived from effete hæmoglobin? This question I hope to discuss in a future paper.

THE BLOOD-FORMING ORGANS AND BLOOD-FORMATION: AN EXPERIMENTAL RESEARCH.

By JOHN LOCKHART GIBSON, M.D., *Formerly Senior Demonstrator of Physiology, University of Edinburgh.*

(Continued from p. 474, vol. xx.)

PART III.—ON THE THYROID GLAND.

WE have now to consider that other organ which has occasionally been called a blood-forming one, namely, the *thyroid gland*: an organ of late brought specially into notice, on the one hand by the writings of Zesas and Credé as to its alleged blood-forming function, and on the other hand by the writings of Kocher and Reverdin as to its other functions, and as to the danger attending its total removal. Here, again, I have by experiment searched for evidence of a blood-forming function; but this time the results have, in contrast with the positive ones got in the case of the bone-marrow, spleen, and lymphatic glands, been wholly negative, that is, do not show the existence of any such function.

To the idea of a possible important blood-forming action of the thyroid, my attention was first directed by the two papers of Zesas already mentioned under extirpation of the spleen. In the last of these papers, Zesas, founding chiefly on an experiment on one dog, though further drawing support from the observations of Credé, concludes that the thyroid is the principal organ which takes the place of the spleen when the spleen is removed, and further says that when the thyroid too is removed then the other blood-forming organs—"lymph-glands and liver (?)"—are unable to make up for the loss of the spleen. (In this paper the researches of Neumann and Bizzozero on the bone-marrow are ignored.)

On reading the above conclusion, I at once saw how insufficiently it was based. For Zesas, in his single experiment, had removed both spleen and thyroid without first having ascertained the effect of removing the thyroid alone.

Accordingly I determined to make experiments as to a blood-forming action, and take care that operation was properly combined with blood-observation. Circumstances, however, for some time prevented this; and when at last I was able to begin I found that other observers were engaged on the subject. Nevertheless, none of their papers came to my notice till I had already excised the thyroid and obtained decided results.

All observers are agreed as to the insufficiency of the grounds on which Zesas came to his conclusion, and all but one are agreed that the reason why the conclusion was so inaccurate was the fact that the removal of the thyroid is in the dog of itself always fatal.

Before Cr  d   and Zesas, the only writer who seems to have made a distinct positive statement as to a functional connection between the thyroid and the spleen is Tiedemann,¹ who said that the spleen is a blood-forming organ, and that after its removal its function is taken over by the thyroid. And with this statement may be contrasted Br  cke's assertion, in his "Vorlesungen   ber Physiologie,"² that while we can refer the spleen to the lymphatic system we know of no connection between the thyroid and that system.

Schiff, who seems to have been the first to pay particular attention to the subject of excision of the thyroid, and who began his experiments in 1856, has lately made further ones,³ which are interesting and in many respects thorough, though they do not seem to have included observation of the blood, apparently because he assumed that the thyroid has nothing to do with blood-formation.

He excised the gland from a number of dogs, and found that when both lobes (or rather, as there is in dogs no isthmus, both glands) were removed at one operation the animals, with but one exception, died between the third and the twenty-seventh day after. The animals became indifferent and melancholic; there was great itching of the skin; at intervals there were fibrillar muscular contractions, followed by clonic and tonic spasms; many had actual tetanus-like attacks; the "excitable zone" of the brain ceased to react to electrical stimulation; and the blood-pressure fell, as a result of vaso-motor paralysis. In the exceptional case the animal had, at the time Schiff wrote, already survived nearly fifty days, and seemed likely to make a permanent recovery.

Afterwards he found that if the lobes, instead of being both removed at one operation, were removed at two operations, separated by a con-

¹ Tiedemann, *Zeitschr. f. Physiologie*, Bd. v. Heft. 1 (1833).—Quoted by Tauber, in *Virchow's Archiv*, Bd. xcvi. p. 30.

² 1. Aufl. (1874), Bd. i. p. 209; and repeated in 3. Aufl. (1881), Bd. i. p. 215.

³ Schiff, "R  sum   d'une s  rie d'exp  riences sur les effets de l'ablation des corps thyro  des," *Revue m  dicale de la Suisse romande*, 15. F  vrier 1884; "R  sum   d'une nouvelle s  rie." *Rev. M  d. de la Suisse rom.*, 15. Aout 1884.

siderable interval (for adult dogs he considers twenty days quite enough), it was then possible to keep the animal alive; and he explains this by supposing that the function of the gland passes over to some other organ or organs, but does so only very slowly. Experimenting as to whether it is to the supra-renal capsules that the function passes, he finds that it is not.

Further, having in a series of experiments placed the freshly-excised thyroid of a dog in the abdomen of another dog, waited from two to five weeks to let it become engrafted, and then removed both lobes of this dog's thyroid at one operation, he found that the dog might, instead of dying like the unprepared dogs from which the whole gland was removed at one operation, survive like the dogs from which the lobes were removed at separate operations.

From the facts obtained, he supposes that the gland may have the function of producing some substance which passes from it into the blood, and there serves as a necessary element in the nutrition of the nervous centres.

Tauber,¹ in a recent paper, holds that Zesas is wrong in saying there is a relation between the spleen and the thyroid. But Tauber's argument proceeds, at least in part, on an erroneous assumption made by him that the thyroid is in domestic animals (cats and dogs?) often entirely wanting.

Another paper on excision of the thyroid is one by two Italian observers, Sanquirico and Canalis,² who likewise disagree with Zesas. They experimented on thirteen dogs. From seven both lobes were removed at the same time, from two both in the course of from six to twenty days, and in four a small portion of the gland was left unexcised.

Their results were—(1) In spite of primary healing, the animals from which both lobes were removed at the same time died in from six to twenty days. (2) The symptoms usually began after from twenty-four hours to three days (in one case only after thirteen days). The animals began to refuse food, swallowed badly, became tired and dyspnoic, suffered from muscular trembling and from general or partial clonic cramps, groaned, and were generally restless. Walking and standing became more difficult, the animals often ran in circles, and they were very apt to fall. In running about they seemed to have a hindrance, as if they had lost control over their movements. On increase of these symptoms followed death. (3) In three cases death was preceded by a fall of temperature from 39° to 35°·5 C. (4) Artificial nourishment failed to prevent death. (5) In some cases purulent conjunctivitis was developed, once with perforating corneal ulcer. (6) Examination of the blood revealed slight changes, which did not, however, overstep physiological limits. (7) *Post mortem* examination

¹ Tauber, "Zur Frage nach der physiologischen Beziehung der Schilddrüse zur Milz," *Virchow's Archiv*, Bd. xcvi. Heft 1 (Apr. 1884).

² Sanquirico and Canalis, "Sulla estirpazione del corpo tiroide," *Archivio per le scienze mediche*, vol. viii. No. 10 (1884). Extracted in *Centralbl. f. klin. Med.*, 18 Oct. 1884.

gave nothing beyond distinct anæmia of both brain substances, often hyperæmia of the liver, and injection of the mesenteric vessels, once with extravasation into the intestinal mucous membrane. (8) Examination of the urine yielded negative results. (9) Both absorption of septic matter and alteration of the vagi or of the recurrent laryngeal nerves could be excluded from consideration as possible causes of death. (10) The animals from which at first only one lobe was removed remained healthy till the other was removed, when the same symptoms appeared as where both were removed at the same time. (11) Two adult animals, from each of which one entire lobe and the upper two-thirds of the other were removed, died, the one after six, and the other after three days. (12) Two from which the spleen had first been removed and one lobe and the lower two-thirds of the other lobe of the thyroid were afterwards removed remained perfectly healthy. (13) One of these two animals having after the extirpation of the spleen been artificially rendered anæmic, an examination of its thyroid, extirpated during full reproduction of the blood, showed no sign of hæmatopoiesis.

And from these facts they conclude—(1) The total extirpation of the thyroid is in dogs absolutely lethal, whether the spleen be removed or not. (2) Spleenless dogs bear partial removal of the thyroid without noteworthy effect. (3) There is no relationship between the spleen and the thyroid. (4) If a small part of the thyroid be left, this is enough to carry on the function of the gland. They cannot as yet say whether the *position* of this remaining part is of importance. (5) The lethal result cannot be ascribed to changes in the blood. (6) The thyroid has nothing to do with blood-formation. (7) It plays an important rôle in the animal economy, standing probably in relation to the nervous system.

Two papers on excision of the thyroid by Dr Julius Wagner,¹ of Vienna, were published in June and July 1884, but came under my notice only after my own experiments were made. He obtained practically the same results as Schiff. His researches were specially directed to the relation of the thyroid to the nervous system, and he does not appear to have paid any attention to the supposition of a blood-forming action. He chose mostly very young animals, expecting that nervous symptoms would be more marked in them.

Wagner draws attention to the fact that dogs are not perfectly suitable for such experiments, inasmuch as they have, in the fat round the arch of the aorta, two small accessory thyroids, called by Wölfler,² who has described them, "aortic glands." And it seems to me quite possible that these glands may occasionally be very well developed, and may account for the case recorded by Bardeleben, where a dog survived after simultaneous removal of both lobes of the thyroid; as well as for one of Zesas' cases (to be afterwards mentioned), where, likewise, the animal seems to have survived, although much affected by the operation. And they may also account for Schiff's success in keeping dogs

¹ Wagner, *Wiener med. Blätter*, 1884, Nos. 25 and 30.

² Wölfler, *Wiener med. Wochenschr.*, 1879, No. 8.

alive when he removed the second lobe at a considerable interval of time after the removal of the first, and thus gave the aortic glands time to hypertrophy.

And, further, there has been another paper by Zesas,¹ in which he has somewhat modified his former conclusions. He experimented on ten dogs and three cats. In most of them the spleen was removed first, and the thyroid subsequently. After the second operation, the animal invariably died. In two cases, however, it lived two months, and thus longer than any of the animals from which other observers had removed the thyroid alone—a fact certainly not in favour of the two organs having a compensatory function with reference to each other. After removal of the thyroid alone, one cat and one dog lived four months, and one dog seems not to have died at all. As to the latter, I have already suggested that it may have been saved by the accessory thyroids ("aortic glands"); and in accordance with this suggestion is the fact, stated by Zesas, that it became very much lowered in condition and very miserable.

In this paper, Zesas, though indeed speaking, on the one hand, of the very distinct symptoms which appear after removal of the thyroid, and, on the other, of the absence of symptoms after removal of the spleen, still holds that the thyroid has an important action in taking the place of the spleen when that organ has been removed. This opinion, however, seems entirely unsupported by his experiments. Certainly the fact that all the animals from which both thyroid and spleen were excised died is no proof of a compensatory function; for it has been clearly shown, even by Zesas' own experiments, that mere removal of the thyroid alone is quite sufficient to cause death.

Zesas says that he found the same changes in the blood after excision of the thyroid as after excision of the spleen, namely, an increase in the number of white corpuscles and a decrease in the number of red; only that these changes appeared later and were less marked. And he further says that if both organs be removed the increase in the number of white corpuscles is enormous. What he means by "enormous" is not stated. Certainly, as will further on be seen, there was no enormous increase of white corpuscles in the blood of a dog from which both organs were removed by myself.

As to the general bearing of my own experiments on the foregoing, I have to say that while these experiments give, so far as I know, the only accurately recorded observations on the blood after excision of the thyroid, they seem to me to show that the removal of the gland produces no direct change in the number of corpuscles. In one case, indeed, there was, shortly before the death of the animal, a decided increase in the number of white corpuscles; but this can, I think, easily be explained in a way quite different from that given by Zesas. For, firstly, Zesas himself mentions that the changes in the blood appeared late; and, secondly, both his observations and those of others show that shortly after the removal of the thyroid the animal refuses

¹ Zesas, "Ist die Entfernung der Schilddrüse ein physiologisch erlaubter Akt?" *Arch. f. klin. Chir.*, Bd. xxx. (1884).

all nourishment; while, thirdly, it has been recorded by Bizzozero and various other observers that when an animal is starved the function of the blood-forming organs comes to a stand-still. So that the very natural explanation of the appearance of an increased number of white corpuscles and a diminished number of red after removal of the thyroid is simply that starvation has occurred, and has caused an inactivity of all the blood-forming organs as regards conversion of white corpuscles into red. To this explanation two of my cases, which were all in dogs, give an interesting support: one (Experiment IX.) showing a still important amount of food and practically no increase of white corpuscles, the other (X.) hardly any food and a decided increase.

Where both spleen and thyroid have been excised, it would of course be quite natural, and in accordance with my explanation, that there should be a still greater increase in the number of white corpuscles and decrease in the number of red than where only spleen or only thyroid has been excised. But, besides being able to say this, I can here, too, bring forward a case which does not even at first sight allow of Zesas' view being taken, namely, one (XI.) where I excised the thyroid more than two months after the spleen had already been excised and yet found in the blood as a result of the excision of the thyroid no alteration whatever. In this case the animal took its food well until the last three or four days of its life.

In this last paper, however, Zesas, while still supporting a blood-forming function of the thyroid, further says that the gland must have some other important function; basing this conclusion on observation of symptoms like those recorded by other writers.

I now pass to a more particular description of my own experiments on excision of the thyroid, which were all, as I have said, on dogs.

Antiseptic precautions were, as usual, observed during the operation; but the wound was not dressed. The wound was sewn up completely, either with chromic-acid catgut or with horse-hair. In all, four operations (on three animals) were performed; if one case be omitted where the animal died of hæmorrhage a few hours after the operation.¹ In three out of the four there was healing by first intention.

The incision was made in the middle line, which enabled one easily to get down between the muscles; and one then found the two lobes, or, rather, separate glands, lying, one on each side, under the sterno-thyroid muscles. Their mobility and slipperiness makes their removal somewhat difficult. As they are separate, the operation is a double one, by means of a single incision.

In the removal of each lobe, first it was drawn out of the wound; then the vessels passing to it were secured with three chromic-acid catgut ligatures, placed, one round those passing to its lower angle (with the tissues surrounding them), another round those passing to

¹ Here is also omitted the case of the animal of Experiment V. In this case, however, only one lobe (or gland) was ever removed.

its upper angle, and the third round the remaining attachments; and lastly all the attachments were divided on the distal side of the ligatures.

From two dogs, A and B, both lobes were removed at the same time; and from the third dog, C, first one lobe, and then, after a month's interval, the other lobe, was removed.

I shall consider first the symptoms common to the two animals, both females, from which both lobes were removed at the same time.

The first animal, A, or that of Experiment IX., was of the English-terrier type and about four months old, and weighed before the operation 2 kilogrammes 80 decagrammes. The second, B, or that of Experiment X., was about eight months old, full-grown, and very strong and well-nourished, and weighed 5 kilogrammes 80 decagrammes.

The first symptoms appeared in from twenty-four to forty-eight hours. The animals became distinctly apathetic and melancholic, showed disinclination to be disturbed, and seemed to have lost the desire for food, being only after considerable coaxing prevailed on to take even milk. Moreover, localised muscular spasms set in, which in A probably appeared first in the œsophagus, when, on the second day after the operation, it cried twice or thrice as if in sharp pain, especially after trying to swallow, and then put its paw into its mouth, as if to remove some offending substance. In both animals an apparent difficulty in swallowing was noticed. General trembling of the body set in very early, and was especially exaggerated when they were disturbed. Frequent fibrillar muscular twitches and a peculiar stiffness of the legs gave the uncertain gait spoken of by Sanquirico and Canalis. There seemed to be itching of the skin, more especially in the face; and pain, as evidenced sometimes by constant, and other times by intermittent groans, presumably caused by the localised cramp-like contractions of the muscles. There seemed to be no pain in the wound; in fact, in A it healed by first intention. A, unlike B, would, after the appearance of symptoms, one day seem quite recovered, and take its food well, and then, next day, again show the symptoms, and appear uneasy and practically refuse all food. B, though much stronger to begin with, showed the symptoms earlier, and without any intermission. In A no general convulsions were observed, but in B they occurred pretty often.

Localised tonic and clonic spasms were common in both. Both seemed giddy when on their legs, and both showed the tendency to walk backwards observed by Wagner.¹ Both lost flesh, more especially B, which in a fortnight was reduced almost to a skeleton. Both died, A thirteen, B seventeen days after the extirpation. The weight of A had been reduced from 2 kilogrammes 80 decagrammes to little more than 2 kilogrammes, and that of B from 5 kilogrammes 80 decagrammes to 3 kilogrammes 45 decagrammes. During the last day or two both were in an almost comatose condition, from which, however, they could easily be roused. Both had inflammation of the conjunctiva; and in one the inflammation was purulent, and before death implicated the cornea. It is interesting to note that Sanquirico and Canalis observed a similar affection of the conjunctiva.

I now proceed to give the enumerations of the blood which were made in these two experiments.

Experiment IX. (A).

	Hæmocytes.	Leucocytes.	Proportion of Leucocytes to Hæmocytes.
Before Operation, . . .	6,470,000	14,000	1 : 462.1
<i>Operation on 24 September 1884.</i>			
26 Sept., 2nd day after, . . .	6,080,000	19,000	1 : 320
27 " 3rd " . . .	6,980,000	15,000	1 : 465.3
29 " 5th " . . .	6,880,000	38,000	1 : 181
30 " 6th " . . .	6,950,000	12,000	1 : 579
1 Oct., 7th " . . .	7,240,000	19,000	1 : 381
3 " 9th " . . .	7,480,000	19,000	1 : 393.6

During the last three days of life no enumeration was made, as the animal was taking no food and was very miserable. Its condition, too, was such that any changes that might then have been found in the number of corpuscles could not have been ascribed to cessation of a blood-forming action of the thyroid.

The results of the enumerations in this case give no real support to the theory of Zesas; for the red corpuscles, after a decrease in number immediately following the operation, again increased, and, with slight irregularities, remained, until the last estimation, at any rate at their former number. The further

¹ *Op. cit.*

increase towards the end, I can ascribe to nothing unless to a diminution of the fluid contents of the vessels; but such a diminution may really have occurred, as the animal not only refused food, but also for the last few days would take neither water nor any other liquid. The number of the white corpuscles cannot be said to have been influenced; for, after the initial rise always observable after an operation, they resumed practically their former number and numerical relation to the red corpuscles. Of the exceptional number found one day, namely, 38,000 per c.m., I can give no explanation.

On the whole case, then, it must be allowed that there was no change in the number of corpuscles sufficient to account for any of the symptoms, and that death must have been due to causes quite apart from the changes found in the blood.

The changes in the blood of B seem to point to the same conclusion.

Experiment X. (B).

	Hæmocytes.	Leucocytes.	Proportion of Leucocytes to Hæmocytes.
Before operation,	8,750,000	19,000	1 : 460·5
<i>Operation on 18 October 1884.</i>			
19 Oct., 1st day after, . . .	7,720,000	28,000	1 : 275·7
21 „ 3rd „	7,240,000	10,000	1 : 724
22 „ 4th „	7,510,000	14,000	1 : 536·4
23 „ 5th „	7,390,000	14,000	1 : 527·8
26 „ 8th „	7,310,000	33,000	1 : 221·5
28 „ 10th „	7,820,000	32,000	1 : 228·7
30 „ 12th „	6,800,000	29,000	1 : 234·4

In this experiment the usual fall in the number of corpuscles after the operation was never recovered from. But this cannot, I think, be ascribed to the removal of a blood-forming organ. It seems really to have been due to starvation, with consequent depression of the blood-forming functions. For the symptoms I have described set in very early, and continued without intermission; and from the day after the operation the animal took hardly any food. And the same explanation will serve for the increase in the number of white corpuscles, and the further decrease in the number of red corpuscles, towards the end of life. In other words, any changes observed in the blood, either in this

experiment or in Experiment IX., could with perfect justice be ascribed to the effect of the removal of the thyroid on the *general* system; and there is nothing in them to support the idea of a direct blood-forming function of the organ.

The case of the third animal, C, gives, likewise, no evidence in favour of a blood-forming function, and also otherwise gives very strong evidence against the supposition that the spleen and thyroid are related in function. The animal was the second one from which the spleen was excised (see Experiment II.). As may be remembered, it, after recovering from a slight ordinary initial fall in the number of red corpuscles, failed to show any other decrease in it until two months after the operation, when there was a distinct and pretty sudden one. It would have been interesting to watch the animal further without submitting it to another operation; but I wished to remove the thyroid from a spleenless animal, in order to watch the effect on the blood, and thought it an unusually good subject for such an experiment, as it had a very well developed thyroid.

I decided to remove first one lobe, and then, after a month's interval, the other. I should have liked to make the interval still longer, in hopes of keeping the animal alive after removal of both spleen and thyroid, as Schiff kept animals after removal of the thyroid alone; but the time at my disposal did not allow me to do so.

Experiment XI. (C).

	Hæmocytes.	Leucocytes.	Proportion of Leucocytes to Hæmocytes.
Before operation, . . .	6,590,000	17,000	1 : 387·6
<i>One lobe excised on 6 January 1885.</i>			
8 Jan., 2nd day after, . .	5,590,000	19,000	1 : 294·5
10 „ 4th „ . .	6,210,000	17,000	1 : 365·2
12 „ 6th „ . .	6,210,000	16,000	1 : 388·1
15 „ 9th „ . .	6,170,000	22,000	1 : 280·4
19 „ 13th „ . .	7,230,000	13,000	1 : 556·1
26 „ 20th „ . .	7,330,000	13,000	1 : 563·8
30 „ 24th „ . .	6,840,000	12,000	1 : 570
6 Feb., 31st „ . .	7,490,000	10,000	1 : 749
<i>Second lobe excised on 7 February.</i>			
11 Feb.,	6,910,000	15,000	1 : 460·6
12 „	6,930,000	17,000	1 : 407·6
16 „	7,240,000	7,000	1 : 1034·2
19 „	6,300,000	12,000	1 : 525

The results of the blood-enumerations will be found in the preceding table.

The removal of the first lobe was followed by no symptom, and it will be noticed that the blood did not suffer. The irregularity in the number of red corpuscles, always, on the average, in the direction of increase, is such as I had already found in my animals after excision of the spleen; and must have been due to irregularity in the blood-forming activity of the bone-marrow and lymph-glands, in their attempts to make up for the loss of the spleen. And it may here further be noticed, as against the supposition of a blood-forming action of the thyroid, that the loss of one lobe did not prevent the blood from being brought up to about the condition in which it was previous to the excision of the spleen (7,520,000 red corpuscles per c.m.) three months before.

Exactly a month after the removal of the first lobe the remaining one was removed, and it was found apparently not increased in size, its weight being the same as that of the first. Both after this operation and after the first one the wound healed by first intention.

For the first few days I hoped the animal would survive. It was quite lively, took its food well, and ran about as usual. Two days after, indeed, there seemed to be a little stiffness in putting down the feet; but one could not be sure, and next day none could be seen. Decided symptoms appeared only on the fourth day after the removal, viz., on the 11th of February. When trying to rise from its bed it at first failed, the hind legs, which had been under it, appearing to be quite stiff; and after it got up it fell once or twice in running across the room. It seemed, however, to recover, and then ran about as usual. But when taken up it trembled a good deal, and fibrillar muscular contractions were likewise evident. On running down stairs it had a slight convulsive attack, like a short epileptic fit. From this day the nervous symptoms gradually developed, although it took its food well until three or four days before its death, and consequently did not lose very much in weight.

The nervous symptoms were very pronounced, and consisted, as in A and B, of almost constant trembling and fibrillar muscular contractions and clonic and tonic convulsions. I saw it in at least two typical epileptic fits, each of which lasted some minutes.

It had also attacks like those of tetanus, with well-marked opisthotonus. The itching of the skin was not very marked. During the last few days of life the animal could hardly be got to come out of its bed, and slept most of the day. When it was disturbed, almost all the muscles became tonically contracted, the head being fixed and the eyes fixed and staring. It did not seem to suffer pain, except during some of the more severe tetanic convulsions, when it cried out. After the fourth or fifth day it had a constant and well-marked expression of hebetude. On the 21st of February, fourteen days after the removal of the second lobe, having made a solution of fresh thyroid gland in a mixture of neutral salts, with the intention of now and then injecting a little into a vein of the animal, to see whether any evidence could be got in support of Schiff's idea that when the substance of the thyroid is absorbed into the blood the animal is preserved in life, I was just preparing to make the first injection, when the animal died, in a strong convulsion.

The animal, as has already been said, took its food well until three or four days before its death; and accordingly the general condition was not reduced to the same extent as in A and B. Its weight on the day of death was 4 kilogrammes 10 decagrammes, the original weight having been 5 kilogrammes.

Post-mortem.—In A and B, from which the thyroid alone had been removed, the *post-mortem* appearances were entirely negative. Distinct anæmia of the brain or spinal cord was not found. The vagi and recurrent laryngeal nerves were perfectly intact. Instead of the spleen showing any sign of blood-formation, it seemed smaller and drier than usual. Unfortunately, I did not notice whether the red bone-marrow had extended into the fatty marrow.

In C, from which both spleen and thyroid had been removed, the *post-mortem* appearances were exactly the same as those in the dog of Experiment I., from which only the spleen had been removed; with this exception, that the lymphatic glands were not enlarged. The red marrow had extended into the shafts of the humerus and femur, and contained a considerable number of nucleated red cells, the marrow in the ribs and in the heads of the long bones being richest in them. Neither in this case nor in the two others could any increase in the size of the liver or excess in its vascularity be observed.

These experiments, taken together with the absence of any sign of haematopoïesis in the thyroid gland of the dogs of my other experiments, or in the second half of the thyroid of the

dogs of Experiments V. and XI., warrant the assertion that the thyroid has apparently no blood-forming function, and that any such function it may really have can only be one extremely subordinate to some other and far more important function. Of any relationship between the spleen and the thyroid gland I have found no sign.

Although the further consideration of the results of excision of the thyroid will be beyond the proposed object of this paper, yet I cannot here refrain from comparing with the observations on animals those which have recently been made on human subjects from whom the whole gland has been removed. For when the two sets of observations are taken together they teach us a very important and most practical lesson, namely, that in the human subject the thyroid should never be removed entirely; but that at any rate a small piece should always be left, if we are to prevent the appearance of symptoms which render the prolongation of life hardly desirable.

Until within the last three or four years surgeons took no particular notice of the isolated cases of tetany which appeared after total excision of the thyroid; and it was only when Weiss,¹ Wölfler,² and Falkson³ showed that a considerable number of the cases of such excision in the clinics of Professor Billroth, in Vienna, and Professor Schönborn, in Königsberg, exhibited symptoms of tetany within a few weeks after the operation, that special attention was drawn to the connection between such symptoms and the particular operation they followed. Some of the patients, after having for days been kept under the influence of narcotics, recovered; and others died. Falkson supposed the tetany to be due to the division of the recurrent laryngeal nerves; but this cannot be the explanation, as the tetany symptoms are very like the convulsive symptoms in dogs after excision of the thyroid, where the recurrent nerves are quite intact. Weiss's paper gives a good account of tetany, and graphically describes two cases of it after excision of the thyroid. Falkson, too, describes the symptoms observed by him, which are very like those in dogs.

The tetany, however, which showed itself soon after the operation, as a rule soon passed off; and it was not until Kocher and Reverdin wrote on cachexia strumipriva that the really serious effect produced by the removal of the whole of the thyroid was pointed out. And even in spite of these writings surgeons are still excising the whole of the thyroid, as if in operating on the gland they need care merely for recovery from the surgical wound.

Kocher took the trouble to ask all his cases of excision (total) of the thyroid to come back and report themselves, and has published the

¹ Weiss, "Ueber Tetanie," *Volkman's Sammlung klinischer Vorträge*, No. 189. (1881.)

² Wölfler, "Die Kropfexstirpationen an Hofrath Billroth's Klinik von 1877-1881," *Wiener med. Wochenschr.*, 1882, No. 1.

³ Falkson, "Zwei Fälle von Tetanie nach Kropfexstirpation," *Berl. klin. Wochenschr.*, 1881, No. 12.

result.¹ He excised the whole gland thirty-four times. Five patients died, viz., three of the operation, and two from unknown causes after healing. Of the others, eighteen presented themselves in person, and six more wrote or were written about. The written accounts do not give evidence of much value. Four of the patients wrote that they were well. The husband of another wrote that his wife's body was swollen and her limbs insensible, that she never felt warm, and that her menstruation was irregular. And the husband of the last of the six wrote that his wife could not write herself, from nervous pain in the hands and feet, which, he said, were almost paralysed. Of the eighteen who presented themselves in person, only two showed no evil effects; and even these two might be said to be only the exceptions which proved the rule. For in one of them there was a small accessory thyroid, which had become enlarged; and in the other there was what Kocher calls a "Strumarecidiv" (relapse of goitre), a small piece of the gland having been left, and having enlarged to about the size of a pigeon's egg. The others all showed more or less interference with the general health, and their symptoms were so much alike that Kocher describes them collectively under the name of "cachexia strumipriva."

The symptoms were as follows:—The patients, as a rule soon after leaving the hospital, but in some cases only four or five months after the operation (Reverdin quotes a case where the time was a year, and Martin one where it was six months), began to complain of tiredness, and especially of weakness and heaviness of the limbs. In many cases the feeling in the limbs amounted to pain. Also, pains in the neck, shoulder, and body were complained of. Then followed a feeling of cold in the extremities, with swelling of the hands and feet, which became of a bluish-red colour, and in winter were very cold and generally frost-bitten. Further, the intellectual activity became diminished, this being especially noticed in children at school, who went down in their class, and in whom their teachers found a constant decrease of mental capacity, even where they had before been the best pupils. Cerebration became very much delayed, a consequent slowness of speech became evident, and even the general movements of the body became slower. In some patients who were servants, the general increase of these symptoms made it necessary for them to leave their places, as they could not get through their work quickly enough. Some patients did not trouble themselves about the symptoms, while others complained of them very much, or had become very retired, because they were conscious of their slowness of cerebration, and that they were not like other people. Moreover, swellings appeared, affecting the face, hands, and feet, and being at first transient, lasting only a few hours, and then disappearing. In one case they appeared only after long pauses; and in that case, while they lasted, the patient suffered from great breathlessness. In many patients the swelling remained, giving their faces a heavy, stupid look, and so making their acquaintances think they had become idiots. The whole face became thicker: the eyelids swollen and transparent, the nose thick, and the lips

¹ Kocher, "Ueber Kropfexstirpation und ihre Folgen," *Arch. f. klin. Chir.*, Bd. xxix.

likewise swollen. The hands and feet, too, and even the body, became permanently swollen; and in two cases there was ascites. The skin over the swollen parts was thick and infiltrated and had lost its elasticity, the surface was dry, and the hair fell out. In advanced cases there was marked anæmia, with a distinct decrease in the number of red corpuscles, and without, in the cases "counted," any distinct increase in the number of white. The minimum number of red corpuscles was 2,168,000, four cases had 2,800,000, five had fewer than 3,500,000, three had fewer than 4,200,000, and two had fewer than 4,500,000. Two cases with slighter symptoms had a pretty normal number, viz., 4,940,000 and 5,520,000. Only one patient with the symptoms at all marked had as many as 4,476,000. Where Kocher made enumerations in cases of partial excision, the number of red corpuscles was found normal. Where at the time of total excision the patient was still growing, the growth was very much retarded. Kocher records that one case had distinct attacks of tetany, and, later, attacks of epilepsy; and, in connexion with this, remarks that many of the other cases had, in addition to the tired feeling already mentioned, also a stiffness of the limbs. The muscles were always well developed; in fact, resembled those of pseudo-hypertrophic paralysis. Fibrillar and localised contractions of the muscles were observed. Kocher says that although the patients looked stupid they were not really idiots, but were capable of recognising and feeling the change in themselves.

Kocher then proceeds to consider whether these symptoms could not be accounted for by the anæmia present, and thinks that the anæmia perhaps gives some support to the idea of a blood-forming function of the thyroid. It seems to me, however, far more likely that the changes in the nervous system were caused *directly* by the removal of the thyroid, and instead of being mere consequences of the anæmia were the causes of it, though it in turn, once developed, would of course intensify them. This explanation is quite borne out by my observations on dogs, where the nervous symptoms made their appearance as the direct result of the excision, and could not be ascribed to anæmia, which did not exist. Moreover, Kocher's own blood-estimations show that in his cases the anæmia made its appearance only after the other symptoms had become developed. And, indeed, Kocher admits that he cannot find proof of the thyroid being a blood-forming organ. If, he says, the thyroid replaces the spleen, why does not the spleen replace the thyroid? In none of his cases could he observe an increase in the size of the spleen. In his last case of total excision of the thyroid he estimated the blood for the first few weeks after the operation, and found no change. And in cases of one-sided excision of the thyroid he was never able to find any subsequent swelling of the remaining lobe.

Further, he tries to account for the anæmia by changes in the trachea. He supposes that the trachea, receiving most of its blood-supply from the thyroideal vessels, is after excision of the thyroid not well nourished; that consequently its walls become softer and its lumen narrower; and that in this way the patients are prevented from getting enough of oxygen—in fact, suffer from an increasing deprivation of it.

This explanation, however, cannot be accepted. In my dogs the trachea was examined particularly, and there was neither softening nor narrowing, and it seemed very fairly supplied with blood. Moreover, both in my dogs and in the animals experimented on by other observers, the shortness of the time the animals survived is against the symptoms having been dependent on narrowing of the trachea. And, to return to human beings, many people go about with the larynx constricted by cicatrices, &c., to a much greater extent than in Kocher's cases the trachea can have been constricted, and yet are able, by a slightly quicker respiration, to make up for the narrowness of the channel.

Other explanations are : (a) the earlier one advanced by Schiff and Liebermeister, that the thyroid regulates the circulation in the brain (a function apparently first suggested by Maignien¹) ; (b) the explanation more recently advanced by Schiff, that the thyroid produces some substance whose absorption into the blood is essential to life ; and (c) the explanation that the thyroid secretes and excretes a substance injurious to the organism, an explanation which has received some support from the experiments of Victor Horsley (see next page).

As to the last of these explanations, a great difficulty in the way of its acceptance is the fact that the thyroid has no excretory duct. And this difficulty does not seem got over by reference to the lymphatics, and their position in close relation to the gland vesicles. For to suppose that the injurious substance is taken up by the lymphatics would involve the improbable-looking further supposition of a passage from these back again into the blood, with a subsequent re-excretion by some other organ.

Of Schiff's two explanations the second seems much the more tenable, as being in accordance both with Schiff's own experiments and with the observations of Sanquirico and Canalis, where only a very small piece of the thyroid was left.

His earlier explanation, that the thyroid regulates the circulation in the brain, seems very insufficient. The theory of such a function is that during great muscular exertion, and consequent violent action of the heart, the pressure of contracted muscles on the jugular and thyroideal veins makes the thyroid become engorged with blood and swell up and thus press on the carotid arteries and prevent overfilling of the cerebral arteries. According to Guyon,² the pressure of the thyroid may even render the branches of the external carotid pulseless. Against this explanation, Schiff's grafting-experiments, where placing the freshly-excised thyroid of a dog in the abdomen of another dog seemed in the case of subsequent excision of the thyroid of this dog to prevent the appearance of symptoms after such excision, would, if confirmed, be conclusive evidence. Moreover, the partial excisions of

¹ Quoted, in 1842, by Longet, in "Anatomie et Physiologie du Système Nerveux," tome i. p. 807.

² Guyon, "Note sur l'arrêt de la circulation carotidienne pendant l'effort prolongé," *Arch. de Physiologie*, t. i. (1868).—Quoted by Nothnagel, in *Ziemssen's Handb. d. spec. Path. u. Ther.*, Bd. xi. 1, p. 6.

Sanquirico and Canalis, where the leaving of one-third of one lobe sufficed for the preservation of life, are greatly against it. And here it may be pointed out that a crucial experiment might be made on dogs. In these animals the vertebral arteries are so large that both carotids may be tied without material injury to the animal, and the experiment would consist in tying both carotids of a dog suffering from the effects of excision of the thyroid. If the symptoms following excision are really due to relief of the carotids from compression by the thyroid, then the ligature of the carotids ought at once to put a stop to them. I regret not having had time to make the experiment, but am very sure that no such effect would have been produced.

In December 1884, in the "Brown Lectures," Victor Horsley¹ described some experiments on monkeys which yielded interesting results. By excising the whole thyroid he produced a condition and symptoms closely resembling those observed by Kocher in human beings, but in some respects intermediate between them and those observed in dogs. He found, moreover, an increased production of mucin in the body generally; and in the case of the salivary glands found not only that those other than the parotid secreted far more than their normal amount of mucin, but also that even the parotid secreted it. He looks on the condition produced by his excisions as being that called *myxoedema* by Ord,² who applied the term to the general swelling in the cretinoid condition that occurs idiopathically in adult women; and he holds that myxoedema, cachexia strumipriva, and cretinism are processes identical in nature. As in cases of excision in human beings, so here too there was anæmia, which Horsley, considering blood-formation one of the functions of the thyroid, attributed to its removal. The animals all died, usually in from five to seven weeks. Horsley's conclusions are: that myxoedema and its allies are due to virtual or actual loss of the thyroid gland; that, however, the *immediate* cause of the changes may be vaso-motor and trophic lesions due to the loss; that the thyroid probably excretes a substance injurious to the organism, and that this substance is of the nature of mucin; that removal of one lobe causes enlargement of the other; and that subsequent removal of the other entails death, after production of the condition and symptoms described by him.

Against the no doubt pretty strong arguments brought forward by Horsley in favour of an excretory function of the thyroid, I may here, besides referring back to the objection already made, of the absence of an excretory duct, also again refer to the apparent success of Schiff in securing dogs against a fatal result of excision of the thyroid by placing the freshly excised thyroid of another dog in the abdominal cavity some weeks before the operation.

With reference to the surgical treatment of diseases of the thyroid, Horsley is reported (*Lancet*) to have condemned total removal of the thyroid, and to have done so on the ground that good results may be obtained by removal of a portion of it.

¹ Report of "Brown Lectures," *Lancet*, 27th Dec. 1884.

² *Lancet*, 27th Oct. 1877.

The conclusions to which my experiments and the observations of others have led me are:—

1. That the thyroid has, properly speaking, no blood-forming function.

2. That any blood-forming action it may in some animals seem to have is due only to the presence of lymph-follicle-tissue in the thyroids of such animals.

3. That its function is in no way compensatory to that of the spleen.

4. That in dogs the total removal of the thyroid is always followed by death, after a definite train of nervous symptoms.

5. That in dogs the presence of unusually well developed aortic thyroid glands may prevent the onset of the symptoms.

6. That the removal of the whole thyroid from the human subject is unjustifiable, such removal being always, after a varying interval, followed by the development of the very serious definite condition called "*cachexia strumipriva*."

7. That in all excisions of the thyroid from the human subject at least a small piece should be left, a small piece appearing to be sufficient for the carrying on of the essential function of the gland.

8. That the function of the thyroid has special relation to the central nervous system, though what the true nature of such relation may be has yet to be definitely determined.

9. That myxoedema, *cachexia strumipriva*, and cretinism are probably one and the same disease, and are due to virtual or actual absence of the thyroid.

Anatomico-Physiological Notices.

PLEXIFORM ARRANGEMENT OF THE CUTANEOUS NERVES IN THE GROIN. By DAVID HEPBURN, M.B., *Senior Demonstrator of Anatomy, University of Edinburgh.*

THE following notes were taken from a dissection performed by Mr R. J. Pope in the Practical Anatomy Rooms of the University of Edinburgh:—

The external cutaneous nerve entered the thigh in its usual position, but soon gave off a branch, which, dividing into two portions, formed communications with the middle cutaneous nerve and the crural branch of the genito-crural nerve.

The genito-crural nerve, in addition to the communication just mentioned, formed two junctions with the middle cutaneous nerve, and these were both found after the latter had pierced the sartorius muscle.

The middle cutaneous nerve had the communications already mentioned, namely, with the external cutaneous and crural branch of the genito-crural. When fully traced to its ultimate distribution, both its inner and outer divisions were seen to pierce the sartorius muscle and thereafter to form junctions with each other.

The internal cutaneous nerve gave off the nerve to the pectineus muscle. In addition, it had three branches of some size distributed in the following manner:—one to the inner side of the thigh at its upper part; another to the inner side of the thigh at its lower part; and the third along the inner edge of the sartorius muscle.

When Scarpa's triangle was fully worked out, the presence of an *accessory obturator nerve* was revealed. It passed outwards over the brim of the pelvis, beneath Poupart's ligament and the pectineus muscle, the latter receiving filaments of supply from the nerve in this position. Small twigs were also supplied to the hip-joint, and in addition it gave off a communicating branch which joined the superficial division of the obturator nerve, and thereafter, emerging from between the pectineus and adductor longus muscles, it passed upwards and outwards beneath the femoral artery and vein, and terminated by joining the internal saphenous nerve about 4 inches from Poupart's ligament.

As the dissection of the front of the thigh proceeded, a thin filament from the external cutaneous nerve was traced downwards over the surface of the sartorius muscle. It entered Hunter's canal, and lay in the connective tissue surrounding the femoral artery. When dissected

from this position it appeared to end in two fine filaments, which were traced into the substance of the vastus internus muscle.

In the popliteal space the obturator nerve was carefully looked for, and it was found lying on the popliteal artery, by which it was carried to the posterior aspect of the knee-joint, which it entered by passing through the ligament of Winslow. From the popliteal space this nerve was traced upwards through the fibres of the adductor magnus muscle, and on the anterior surface of this muscle it was found to be continuous with the deep division of the obturator nerve.

NOTE OF A CASE OF ABSENCE OF VAGINA, WITH UNDEVELOPED UTERUS AND OVARIES. By J. A. CAMPBELL M.D., F.R.S.E.

S. W., æt. 27, was admitted into the Carlisle Asylum in January 1877. She was stated to have been insane for seven years, and at intervals to have taken epileptic fits. She had never menstruated. Her mental state had alternated between excitement and depression, and she was said to have shown erotic tendencies during the periods of excitement, and to have been in the habit of exposing her person at such times. The doctor who attended her wrote to me to say that he thought she had an abdominal tumour, due to retained *meneses* from imperfect *hymen*, and that I should look to this at once as a possible cause of her state.

On admission, a full examination of her mental condition and physical state was made and recorded. I quote the following:—"She was undersized, had a low type of face, her lungs and heart were normal, and nothing abnormal was detected as regards abdominal viscera; her mammae were well developed. She had much hair over *pubes*; her external genital organs were well developed, but no vagina could be found." Owing to the expressed opinion of her former medical attendant, I asked Mr Page of Carlisle to examine her with me a few days after her admission. We agreed that no abdominal tumour existed; that though the external genital organs were normal, there was an absence or occlusion of the vagina, a white glistening structure forming an impervious *cul-de-sac* where the opening of the vagina should have been. A catheter passed into the bladder could, by rectal examination, be distinctly felt without the intervention of anything corresponding to a uterus.

The patient lived in the asylum for nine years, never menstruated, was examined on one or two occasions without anything further being made out. She had epileptic fits of a severe character at considerable intervals, and had attacks of excitement at short intervals of three, four, or five weeks, and at such periods she exhibited erotic tendencies, stripped off her clothes, and exposed her person. She ultimately developed phthisis, and died of this disease.

Autopsy.—The viscera occupying the different cavities were carefully examined and their state recorded. I need only mention that tubercular deposit of lungs and ulcers of intestines caused death.

The external genital organs showed the appearances noted in the case. The internal organs of reproduction were almost undeveloped. The ovaries—very small, shrivelled, and indurated—occupied a normal position. The Fallopian tubes communicated with a rudimentary uterus about seven-eighths of an inch in length. So far as could be made out, it was devoid of an os, and lay very low in the pelvis. Examination failed to show any communication between uterus and external genital organs.

Remarks.—Though I am quite aware such cases are not unknown, yet they are of sufficient rarity to make it worth while putting such a case on record. It is, I think, highly probable that the attacks of excitement occurred at what would, under other circumstances, have been monthly periods. A degree of sexual excitement was distinctly present in the case.

If the ovaries shed ova, what became of them?

NOTES ON AN ABNORMAL ARRANGEMENT OF THE
LARGE INTESTINE. By B. C. A. WINDLE, M.A., M.D.,
Professor of Anatomy in the Queen's College, Birmingham.

THE following unusual arrangement of the large intestine was observed in a male subject recently examined in my dissecting room, and may be of interest when taken in conjunction with the papers which have appeared in the *Journal of Anatomy and Physiology*, and with Mr Treves' recent lectures on the Anatomy of the Human Intestinal Canal and Peritoneum.

The cæcum was large and placed entirely above the margin of the ilium. It did not come into contact at all in its attachments with the posterior wall of the abdomen. The vermiform appendix lay on the iliacus muscle, and was directed downwards and outwards. The colon passed at first directly backward to reach the posterior wall, which it did just above the crest of the ilium. From this point it pursued its ordinary course until it arrived at the crest of the left ilium. Here it seemed to sink into a kind of peritoneal pocket, formed by a process passing from the anterior lateral wall to the anterior and inferior surface of the colon, which turned upon itself here, and ascended along the posterior wall of the abdomen on the right side of the descending colon. It was included in the same fold of peritoneum, and into the neck of the fold passed the sigmoid artery, which broke up into two sets of branches to supply the two tubes. Arrived at the splenic flexure, the ascending tube was held firmly in position by a process of peritoneum passing from the sustentaculum lienæ, which was exceptionally strong, including the splenic flexure of the trans-

verse and descending colon, and passing on to the second tube. The free edge of this process formed the margin of a deep and capacious pouch, whose concavity was directed to the right side of the abdomen. From this point the colon again descended, and was again, but to a much smaller extent, looped up by a band of peritoneum passing to it from in front of the left side of the vertebral column close to the duodeno-jejunal fold. The free margin of this band also marked off a pouch of less dimension than the first mentioned, the direction of whose concavity was similar to that of the larger, in which it was included. The colon after this small loop passed down in a nearly straight line to the rectum. In this course it was bound to the posterior wall close to the vertebral column by a fold of peritoneum, the line of reflection of which on either side was nearly straight. There were thus three tubes of large intestine throughout the entire length of the left side of the abdomen, two descending and one ascending. The peritoneum on the posterior wall was somewhat roughened, and there were a few evidently morbid adhesions between the coils of intestine. These were, however, quite different from the true process, in which the first mentioned two tubes were included.

A NEW METHOD FOR THE QUANTITATIVE ESTIMATION OF URIC ACID. By JOHN B. HAYCRAFT, M.B., B.Sc., F.R.S.E., *Professor of Physiology, Mason and Queen's Colleges, Birmingham.*

WISHING to continue a research upon albuminoid metabolism, and having been much disheartened by the unsatisfactory nature of the processes used for the estimation of uric acid, I determined, if possible, to introduce one which should be at the same time exact and easy of application.

The method of Heintz is certainly not very reliable, and is not applicable when small quantities of the acid are present in the urine. Salkowski's modification, although certainly more reliable, is far too laborious, and is not free from other objections. The same may be said of a somewhat similar process introduced by Fokker. Other methods, depending on the power which the acid has of reducing certain metallic salts, or upon the decomposition of the uric acid, and the collection of its decomposition products, I tried, but soon had to give them up. Inasmuch as uric acid forms some salts more insoluble than itself, and as some of these are with metals easy of estimation, it occurred to me that it might be possible to precipitate it as a salt, say of lead, barium, or silver; and then, by estimating the metal in the precipitate, to calculate the uric acid in combination with it.

Many experiments were undertaken with the uric acid salts of barium, mercury, and lead; their solubilities in various acids, &c., were tested; and endeavours were made to separate (in these forms)

the acid from solutions of mixed salts and other compounds found in urine, and likely to interfere with the process. One or two rough methods were devised, but were soon discarded from their want of accuracy. An attempt to separate out uric acid as a silver salt was more successful.

Urate of silver is, as is well known, very insoluble in water. I find it to be very soluble in 20 per cent. nitric acid, and in somewhat stronger sulphuric acid. It is insoluble in ammonia, and almost insoluble in strong acetic acid.

After a futile attempt to separate out the uric acid from the phosphates of the urine, after acidulation with acetic acid, I succeeded in elaborating the following process:—

The fact that urate of silver is insoluble in ammonia water is a very curious one, inasmuch as this is a solvent for nearly all the silver salts—for example, the chlorides, phosphates, and oxalates. On adding a solution of silver nitrate to a solution of acid urate of sodium, I found that, instead of a precipitation of silver urate, an immediate reduction occurred, the black precipitate not re-dissolving in ammonia water. If, however, the solutions be previously rendered ammoniacal, a white gelatinous precipitate of the urate at once forms. The silver, however, becomes partially reduced before it is possible to collect and wash it. I find, however, that the previous addition of bicarbonate of sodium prevents this reduction. The same obtains with the acid urate of sodium normally present in urine, the chlorides and phosphates remaining in solution, the urate of silver alone falling on the addition of the ammoniacal nitrate. In order to estimate the silver in this precipitate of the urate, the latter was collected in a filter, and washed with distilled water, and taking advantage of its ready solubility in nitric acid, it was dissolved in that reagent.

A method not long introduced by Volhard,¹ and one which is available for the estimation of silver in an acid medium, was used as the final step of the process.

The only difficulty that occurs is in filtering and washing the precipitate of urate of silver. It is gelatinous, and clogs up the filter. It is imperative to use a Sprengel's pump, and a properly made asbestos filter is advisable. In this case, the whole process may be completed in little more than half an hour. The filter should be prepared in the following way:—A small funnel is half filled with broken glass. A sufficient quantity of asbestos is shaken in a flask with water until all the fibres have separated, forming a uniform pulp. This is poured on the glass, and should form an uniform felt, one quarter of an inch thick. The filter can be used again and again for several analyses.

DESCRIPTION OF METHOD.

Solutions Required.—1. Centinormal ammoniac sulphocyanate. Dissolve about 8 grammes of crystals in a litre of water, and adjust it to

¹ "Die Anwendung des Schwefelcyammoniums in der Maassanalyse," Liebig's *Annalen*, Band cxc. p. 1. See also Sutton's *Volumetric Analysis*.

decinormal silver solution. Dilute with 9 volumes of water. One cubic centimetre is equivalent to 0·00168 of uric acid.

2. A saturated solution of iron alum.

3. Pure nitric acid (20–30 per cent.). Dilute the commercial acid, boil and preserve from light in a blackened flask.

4. Strong ammonia.

5. Ammoniacal silver solution. Dissolve 5 grammes of nitrate in 100 cubic centimetres water, and add ammonia, until the solution becomes clear.

Process.—Measure off 25 cubic centimetres of urine in a pipette, and place it in a small beaker, with about 1 gramme of bicarbonate of sodium. Add 2 or 3 cubic centimetres of ammonia, which will produce a precipitate of ammonia-magnesium phosphate. On adding 1 to 2 cubic centimetres of the ammoniacal silver solution, the uric acid falls as a white gelatinous precipitate of urate of silver.

This is collected on the asbestos filter, and carefully washed, until the washings give no trace of silver, with a drop of salt solution. The urate is then washed through the filter by the aid of a few cubic centimetres of the nitric acid, and the silver in this solution estimated by Volhard's method.

Add a few drops of the saturated solution of iron alum, which is the indicator, and drop in the centinormal solution of ammonic sulphocyanate. A white precipitate will form, together with a transient reddish coloration, which latter becomes permanent when the process is at an end.

It is easy to calculate the uric acid, which will be the number of cubic centimetres of the sulphocyanate used multiplied by 0·00168.

If the urine contain albumen, this should previously be removed. If uric acid or urates be present in such quantity as to cause turbidity, the secretion should be warmed and diluted.

In order to test the accuracy of the process, I prepared several solutions of acid urate of sodium of known strength. To these I added various quantities of common salt, sulphate of magnesia, and phosphate of soda, in order to imitate, as far as possible, the urinary secretion. On estimating the uric acid in these solutions, I obtained wonderfully correct results, as the subjoined tables will show. In all cases a quantity not much more than a milligramme was lost during the process, and may be simply accounted for by the fact that no salt of uric acid is absolutely insoluble.

	Experiment 1.	Experiment 2.	Experiment 3.
Uric acid present as urate, .	0·0486	0·0459	0·0211
Uric acid found, .	0·0470	0·0437	0·0198
Loss during process, .	0·0016	0·0022	0·0013
	3 per cent.	5 per cent.	6 per cent. loss.

In order further to test its accuracy, 50 cubic centimetres of urine were divided into two equal portions; to the first, 25 cubic centimetres of a solution of acid urate of sodium of known strength were added; to the second, 25 cubic centimetres of water were added.

When estimated, the two fluids should show a difference equal to the quantity of the salt added.

	Experiment 1.	Experiment 2.	Experiment 3.
Uric acid found (a), . . .	0·034	0·026	0·041
Uric acid found (b), . . .	0·0144	0·0105	0·0254
Difference,	0·0196	0·0155	0·0156
Uric acid added,	0·021	0·016	0·0160

The above figures show how delicate the process is, and what accurate results may be obtained from its use. This depends, in the first case, on the great insolubility of the silver urate; and secondly, on the great delicacy of the final estimation of the silver by the ammonic sulphocyanate. It may be objected to this process that there may be other substances present in the urine which may form compounds with the silver nitrate, thus vitiating the result. Xanthin, as is well known, combines with silver. This substance may be present in small quantities, but its silver compound is, I find, insoluble in nitric acid. I am aware of no substance present in urine normally, or likely to appear as an abnormality, which forms a combination with silver both insoluble in ammonia and soluble in nitric acid.

I should probably have tried much sooner the separation of the uric acid as a silver-salt, but for a statement of Salkowski's.¹ This distinguished chemist analysed the precipitate which forms after adding ammoniacal nitrate of silver to urine. He found a variable quantity of both silver and magnesia, and concluded from this that the uric acid precipitates out, both as an urate of magnesium and an urate of silver. In this case, I could not, of course, use the silver process for its estimation. His facts may otherwise be explained. As is well known, ammonio-magnesium phosphate separates out slowly. Salkowski, immediately after the addition of ammonia, filtered off the ammonio-magnesium phosphate, and then added silver-nitrate. Probably, with the urate of silver, a small and variable quantity of the double phosphate came down, for this would probably be not yet entirely precipitated. As to the variable quantity of silver, this is easy to account for. In my own investigations, I attempted at one time to estimate the uric acid by its reducing action on silver (a method which was quite unsatisfactory), and I found that the same quantity of urate reduced a very variable quantity of silver, depending upon two factors—time and temperature. With prolonged boiling, as many as four parts of silver are reduced by one of the urate. Now, in Salkowski's investigations, the reduction of the silver was disregarded (for he speaks of the black precipitate on the filter-paper). The amount of the reduction would not be the same in any two experiments. In my own method, all reduction is prevented by the addition of the bicarbonate of sodium. I have since added to urine large quantities of magnesium-sulphate, without interfering with the accuracy of the results.

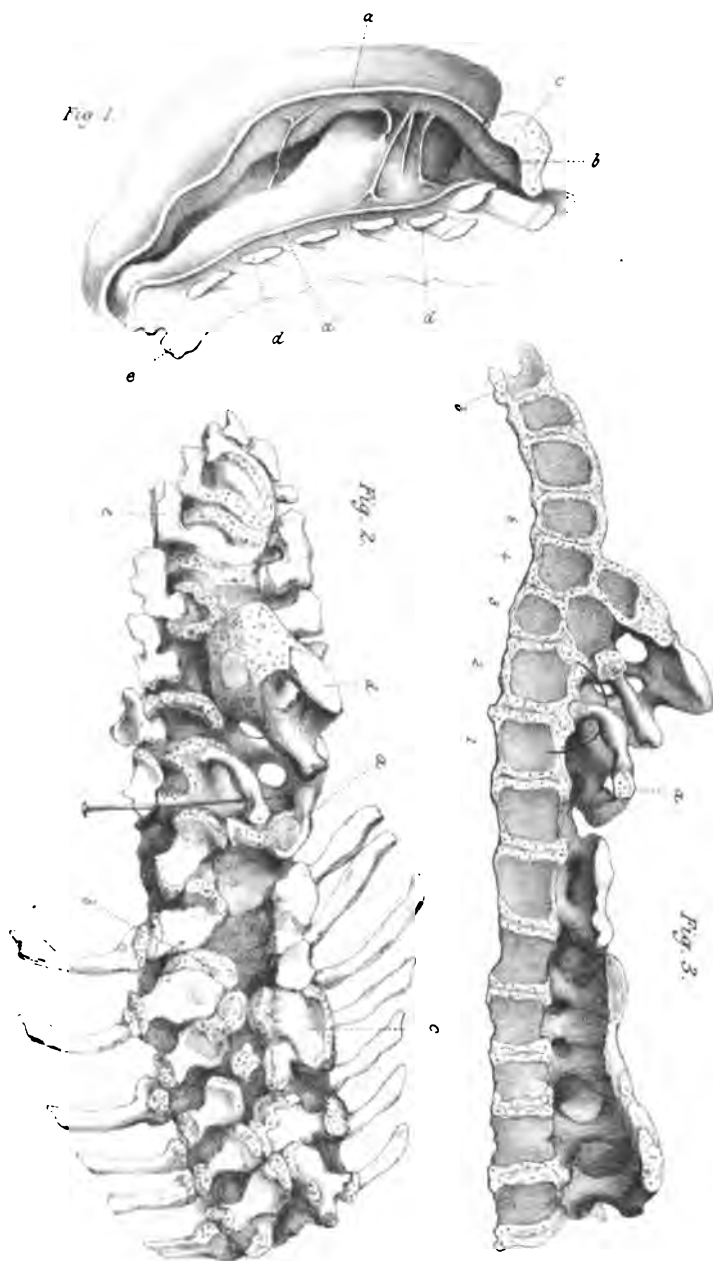
This method was elaborated during the year 1883. I have much pleasure in expressing my indebtedness to the Scientific Grants Committee of the British Medical Association for assistance in the shape of a grant to cover my expenses.

¹ Pflüger's *Archiv.*, B. 5, p. 210.

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SPINA BIFIDA.

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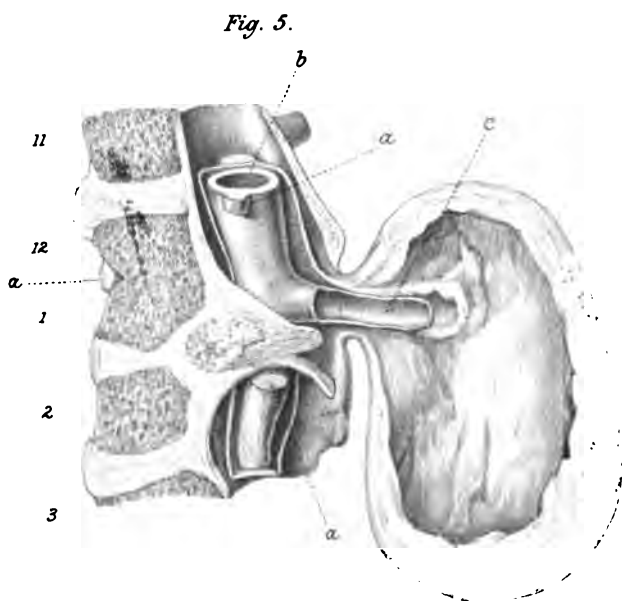
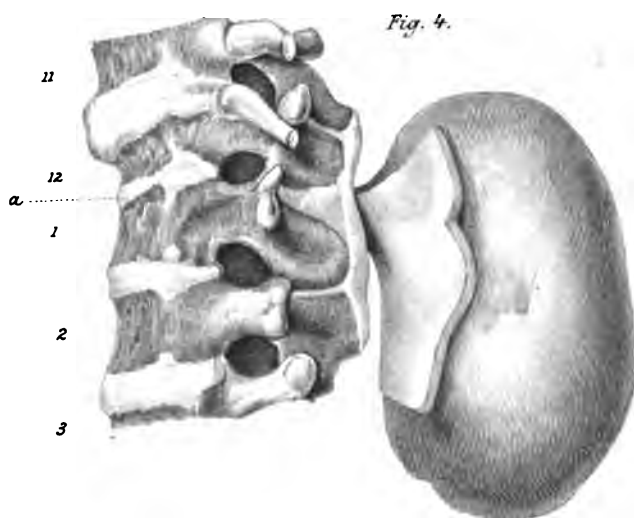


Fig. 1

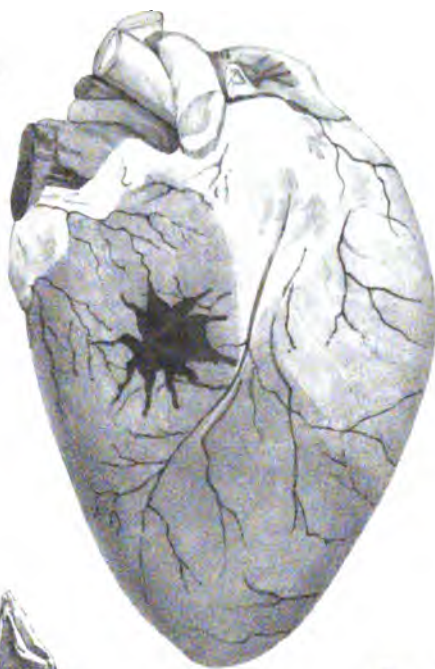


Fig. 2.

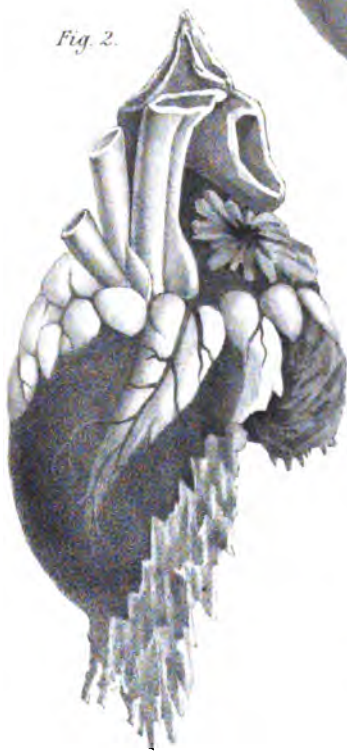
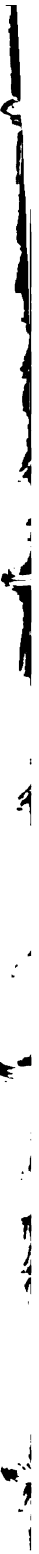


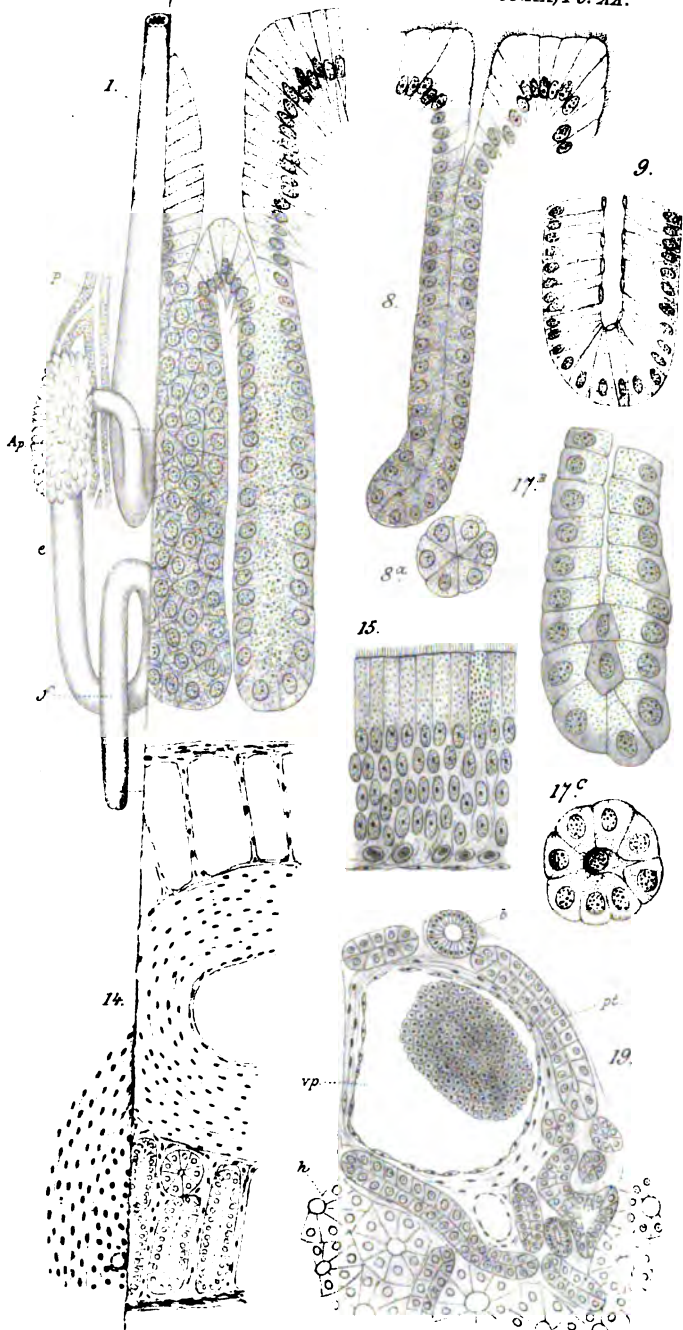
Fig. 3.



W O U N D E D H E A R T .

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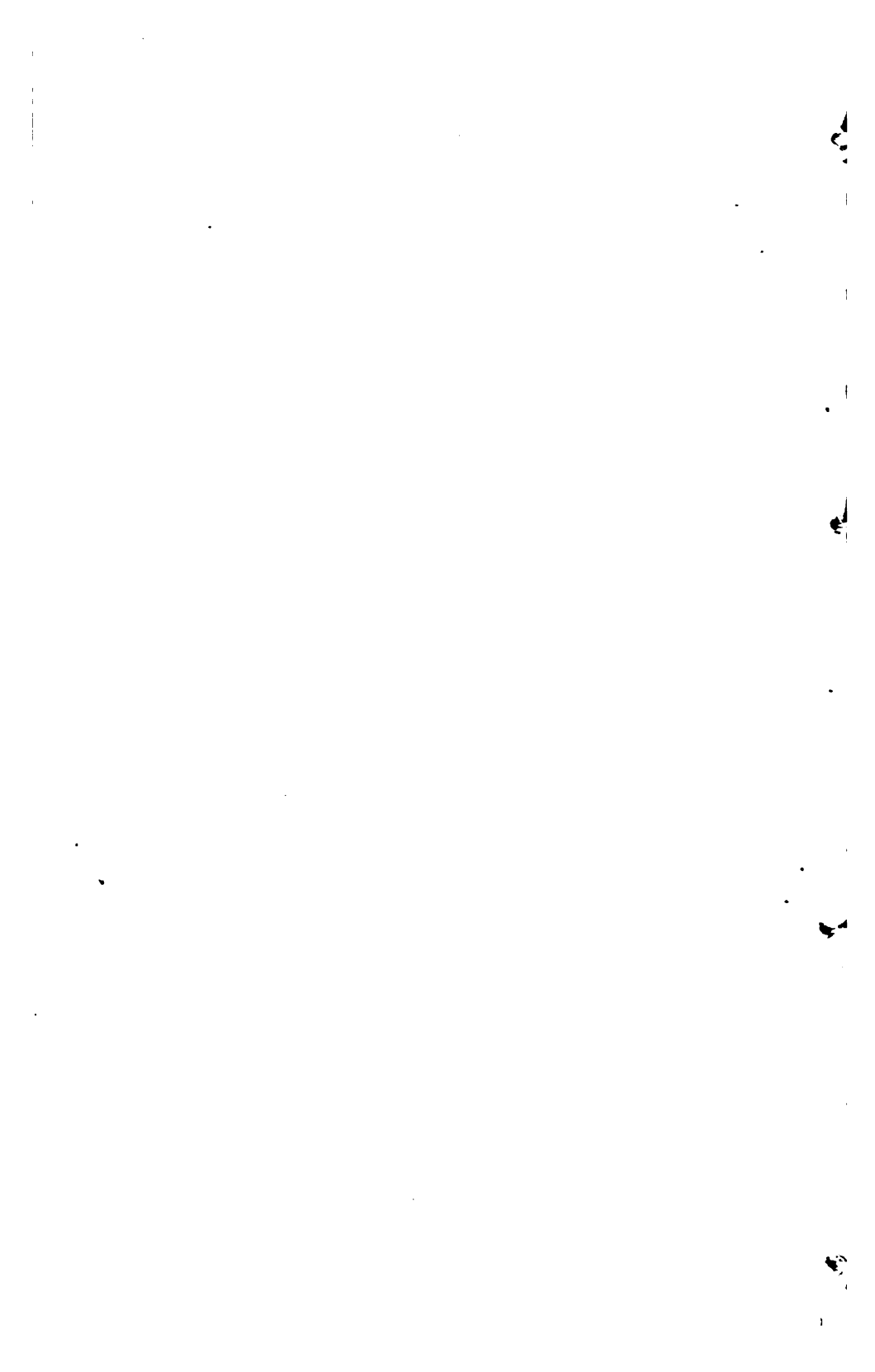


Fig. 4.

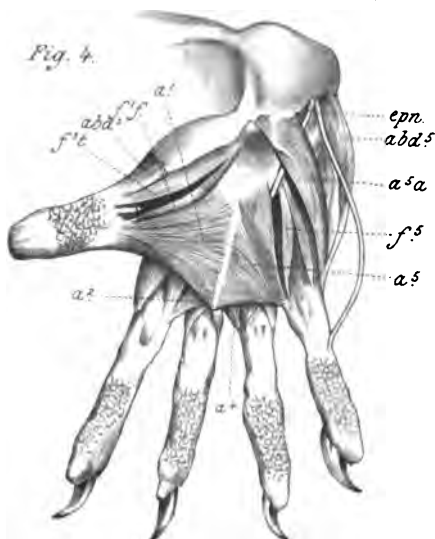


Fig. 8.

